Program and Abstract of International Symposium: "Evolution of the Tertiary Primates in Asia

Asian Paleoprimatology

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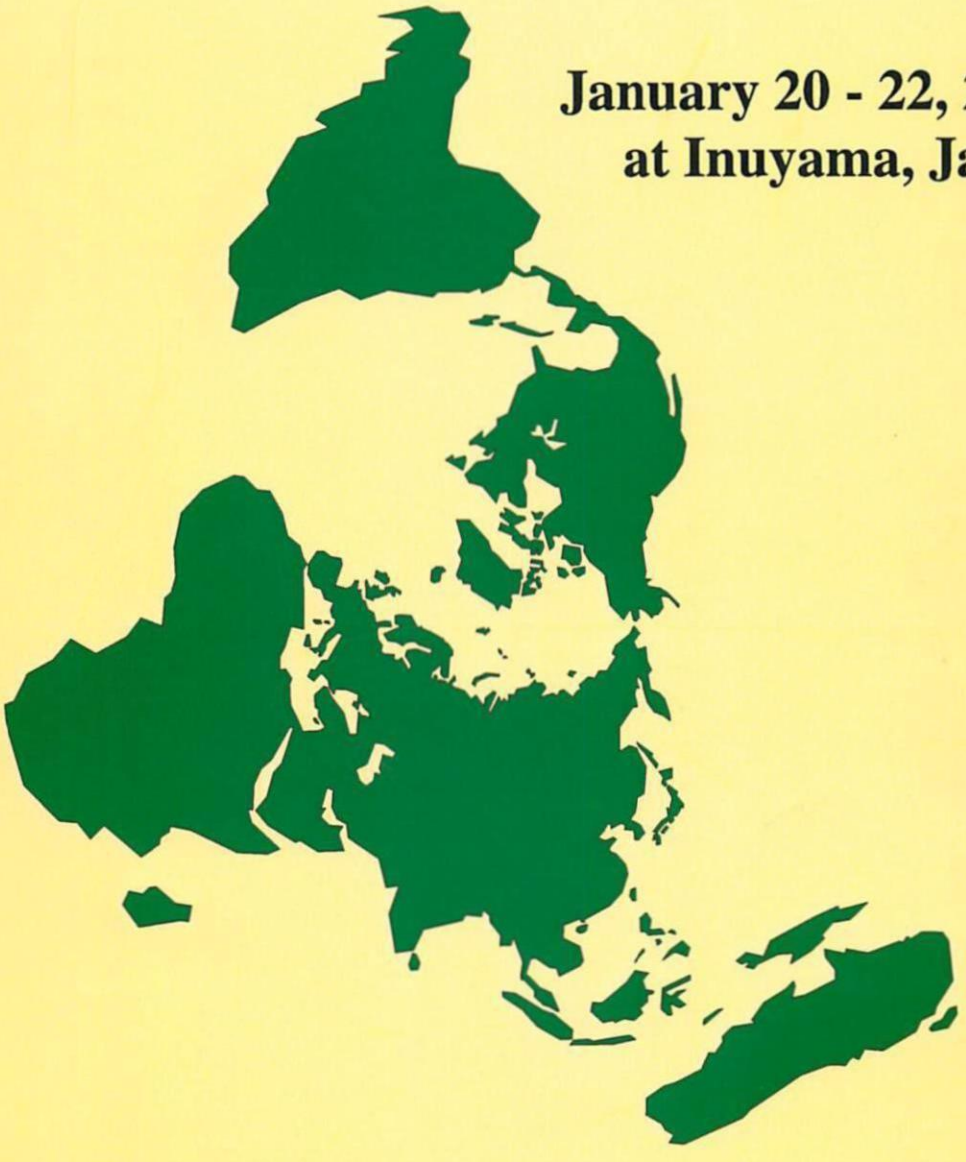
"Evolution of the Tertiary Primates in Asia"

January 20 - 22, 2003
at Inuyama, Japan



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「東アジアにおける霊長類の進化」講演予稿集

Primate Research Institute, Kyoto University

International Symposium

Asian Paleoprimatology

- Evolution of the Tertiary Primates in Asia -

January 20 – 22, 2002.12.26
at Inuyama, Aichi, Japan

Organizing Committee

Nobuo Shigehara
Masanaru Takai
Yutaka Kunimatsu
Hitomi Hongo
Michael A. Huffman

Sponsored by the Ministry of Education, Culture, Sports, Science and Technology in cooperation with Inuyama City

Hosted by Primate Research Institute, Kyoto University, Inuyama, 484-8506, Japan
tel & fax: 0568-63-0536; e-mail: takai@pri.kyoto-u.ac.jp, or huffman@pri.kyoto-u.ac.jp

PARTICIPANTS

K. Christopher Beard

Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213, U.S.A.

David R. Begun

Department of Anthropology, University of Toronto, Toronto, ON M5S 3G3, Canada

David Cameron

Department of Anatomy and Histology, The University of Sydney, 2006, Australia

Yaowalak Chaimanee

Paleontology Section, Geological Survey Division, Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand

Eric Delson

Department of Vertebrate Paleontology American Museum of Natural History, New York, NY 10024

Naoko Egi

Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

Daniel L. Gebo

Department of Anthropology, Northern Illinois University, DeKalb, IL 60115, U.S.A.

Guo Jianwei

The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P. O. Box 643, Beijing 100044, China

Terry Harrison

Department of Anthropology, New York University, 25 Waverly Place, New York, NY

10003, U.S.A.

Yoshikazu Hasegawa
Gunma Museum of Natural History, Tomioka, Gunma, Japan

Mitsuo Iwamoto
Japan Monkey Centre, Inuyama, Aichi, Japan

Nina G. Jablonski
Department of Anthropology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599, U.S.A.

Jean-Jacques Jaeger
Institut des Sciences de l'Evolution, Université Montpellier II, CC 064-Palace E. Bataillon, 34095-Montpellier Cedex 05, France

J. Kappelman

Richard F. Kay
Department of Biological Anthropology and Anatomy, Duke University Medical Center, PO Box 3170, Durham, NC 27710, U.S.A.

Jay Kelley
University of Illinois, Chicago, U.S.A.

Akihiro Koizumi
Iida-City Art Museum, Iida, Nagano, Japan

Yutaka Kunimatsu
Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

Liu Wu
The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P. O. Box 643, Beijing 100044, China

M. Maga

Evgeny N. Maschenko
Russian Academy of Science, Moscow , Russia

Maung Maung
Mandalay University, Mandalay, Myanmar

Shinji Nagaoka
Nagasaki University, Nagasaki, Japan

Hideo Nakaya
Kagawa University, Takamatsu, Japan

Ni Xijun
The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P. O. Box 643, Beijing 100044, China

Sherry Nelson
University of Michigan, Ann Arbor, U.S.A.

Pan Yuerong
The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P. O. Box 643, Beijing 100044, China

Rajeeb Patnaik
Center of Advanced Study in Geology, Panjab University, Chandigarh-160014, India

Martin Pickford

Chaire de Paléoanthropologie et de Préhistoire du Collège de France, GDR 983 et UMR 8569 du CNRS, 8, rue Buffon, 75005 Paris, e-mail : pickford@mnhn.fr

Qi Tao

The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P. O. Box 643, Beijing 100044, China

Benjavun Ratanasthien

Chiang Mai University, Chiang Mai, Thailand

Brian G. Richmond

Department of Anthropology, George Washington University 2110 G St, NW, Washington, DC 20052, U.S.A.

Haruo Saegusa

Himeji Institute of Technology, Sanda, Japan

Nobuo Shigehara

Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

Brigitte Senut

Laboratoire de Paléontologie du Muséum National d'Histoire Naturelle, GDR 983 et UMR 8569 du CNRS, 8, rue Buffon, 75005 Paris, e-mail : bsenut@mnhn.fr

Rodolphe Tabuce

Institut des Sciences de l'Evolution, Université Montpellier II, CC 064-Palace E. Bataillon, 34095-Montpellier Cedex 05, France

Masanaru Takai

Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

Takehisa Tsubamoto

Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

Akiko Uchida

Department of Literature, Chiba University, Chiba 263-8522, Japan

Vu The Long

National Center for Social Sciences and Humanities of Vietnam, Institute of Archaeology, 61 Phan Chu Trinh, Hanoi, Vietnam

Zhao Lingxia

The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P. O. Box 643, Beijing 100044, China

Zheng Liang

Provincial Institute of Archaeology, Kunming 650118, China

PROGRAM

January 20 PM: Paleogene primates

13:30 – 13:45 Opening Remark

13:45 – 14:15 **Ni Xijun** "A Skull of *Teilhardina* from the earliest Eocene of China"

14:15 – 14:30 **Maung Maung** "Stratigraphy and geologic age of the primate-bearing Pondaung Formation at Paukkaung area, Myanmar"

14:30 –15:00 **M. Takai, T. Tsubamoto, N. Egi, & N. Shigehara** "The Pondaung primates in relationship to the faunal transition during the middle/late Eocene in East Asia"

15:00 – 15:30 COFFEE BREAK

15:30 – 16:00 **Y. Chaimanee** "The contribution of Thailand for the understanding of primate evolution in SE Asia"

16:00 – 16:30 **J.-J. Jaeger** "The Importance of South Asia in the Evolution of Anthropoid Primates : Facts and guesses"

16:30 – 17:00 **R. Tabuce** "New Middle Eocene primates and afrotheres from northwestern Africa and their contribution to the understanding of African-Asian faunal exchanges"

18:00 – 20:00 WELCOME PARTY (at "Freude")

January 21 AM: primitive catarrhines

9:30 – 10:00 **R. F. Kay** "The adaptations of *Pondaungia* and *Amphipithecus*, South Asian late Eocene primate"

10:00 – 10:30 **K. C. Beard** "Discovery of a new Clade of Asian Primates from the late Eocene of the Baise Basin (Guangxi Zhuang Autonomous Region, People's Republic of China): The Impact of Global Climate Change on Primate Phylogeny and Biogeography"

10:30 – 11:00 COFFEE BREAK

11:00 – 11:30 **T. Harrison** "The zoogeographic and phylogenetic relationships of early catarrhine primates in Asia"

11:30 – 12:00 **Pan Yuerong** "New material of small-sized primates from the Late Miocene of the Yuanmou, Yunnan"

12:15 – 13:30 LUNCH

January 21 PM: Asian hominoids 1

13:30 – 14:00 **D. R. Begun** " East is east and west is west: Relations among European and Asian Miocene hominids "

14:00 – 14:30 **B. G. Richmond, J. Kappelman, & M. Maga** "Postcranial fossils of *Ankarapithecus meteai* and the evolution of hominoid locomotion"

14:30 –14:45 COFFEE BREAK

14:45 – 15:15 **R. Patnaik & D. Cameron** "Evolution and Extinction of Siwalik Fossil Apes: A review based on new palaeoecological and palaeoclimatological data"

15:15 – 15:45 **J. Kelley** "Late Miocene Asian hominoids and orangutan ancestry"

15:45 – 16:15 **S. Nelson** "The preferred habitats of *Sivapithecus* and paleoenviromental changes leading to its extinction in the Siwaliks of Pakistan"

16:15 – 16:30 COFFEE BREAK

16:30 – 17:00 **Liu Wu & Zheng Liang** "The comparisons of tooth size and morphology between the late Miocene hominoids from Lufeng and Yuanmou, and the implications for their diet, behavior and environment"

17:00 –17:30 **Zhao Lingxia** "Study on enamel microstructure of Late Miocene hominoids from Yunnan of China"

18:00 – 20:00 DINNER

January 22 AM: Asian hominoids 2

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9:30 – 10:00 **Y. Kunimatsu, B. Ratanasthien, H. Nakaya, H. Saegusa, & S. Nagaoka** "Hominoid fossils discovered from Chiang Muan, northern Thailand: The first step towards the understanding of the hominoid evolution in the Neogene Southeast Asia"

10:00 –10:30 **M. Pickford and B. Senut** "Ape lower molars with chimpanzee- and gorilla-like features from the late Middle Miocene and late Miocene of Kenya: Implications for the chronology of the ape-human divergence and biogeography of Miocene hominoids"

10:30 – 11:00 COFFEE BREAK

11:00 – 11:30 **Vu The Long** "The Orangutan fossils in Vietnam"

11:30 – 12:00 **E. Delson** "Hominidae other than Ponginae in eastern Asia: an updated survey" and "*Procynocephalus*, a large cercopithecine from the east Asian Pliocene and Pleistocene, and its relationship to western Eurasian *Paradolichopithecus*"

12:00 – 13:30 LUNCH

January 22 PM: Old World monkeys

13:30 – 14:00 **E. N. Maschenko** "Evolutionary history of colobine monkeys in the Transbaikalian Province"

14:00 – 14:30 **N. G. Jablonski** "Forest Refugia and the Evolution of Primates During the Tertiary and Quaternary in East Asia"

14:30 – 15:00 **M. Iwamoto, Y. Hasegawa, & A. Koizumi** "A Pliocene Colobine Skull from the Nakatsu Group, Kanagawa, Japan"

15:00 – 15:30 COFFEE BREAK

15:30 – 16:30 Discussion and closing remarks

18:30 – 20:30 Dinner

ABSTRACTS (Oral Session)

A Skull of *Teilhardina* from the earliest Eocene of China

NI Xijun, HU Yaoming, WANG Yuanqing, & LI Chuankui

The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, China

Great amount of fossil evidences indicate that the early Eocene is the key epoch for the origin and diversification of euprimates. *Teilhardina* is the most nearly generalized omomyids and is very near to the base of the first radiation of euprimates. The type species of *Teilhardina*, *T. belgica*, is recorded from the earliest early Eocene of Belgium and France (Teilhard de Chardin, 1927; Russell *et al.*, 1967), and it is the only known species of the genus in Europe. More discoveries and well-documented specimens indicate that *Teilhardina* is more diversified in North America than in Europe (Bown & Rose, 1987; Gingerich, 1993; Rose, 1995). In Asia, the knowledge on early euprimates is rather limited. Recent discoveries of euprimates from the early-middle Eocene of China show great significance for the discussion about the origin and evolution of the group. Now, a new discovery from China will expand the euprimate *Teilhardina*'s distribution range to Asia, and the new record will fill the early euprimates' chronological and zoogeographic gaps.

New *Teilhardina* materials were unearthed from upper section of the Lingcha Formation in Hengyang Basin, Hunan Province, China. Fossil mammalian fauna from the locality was correlated with Bumbanian of Asia, Wasatchian of North America and Sparnacian of Europe Land Mammal Ages (Russell & Zhai, 1987). Recent isotope stratigraphy, magnetostratigraphy, and quantitative biochronology research reveal that the upper part of the Lingcha Formation is just at the Paleocene / Eocene boundary with an estimated age of 54.97 Ma (Bowen, G. J. *et al.*, 2002).

The new materials include a damaged skull and two fragments of lower jaws, which belong to the same individual, an isolated lower incisor and another two fragments of lower

jaws. It hitherto is the earliest euprimate with skull preserved. Although the skull is badly damaged, kept frontal and parietal bones show that the brain case is round and large. The orbits are moderate in size. Two orbits are obviously convergent. Postorbital septum may be lacking. The nasal region is narrow and short. One lower jaw is nearly completely preserved. Its horizontal ramus is low, straight and flat stick-like. Its coronoid and condylar processes are broad, thin and rather high. And its angular process is prominent.

The dental morphology of the new material fits the diagnosis of the genus *Teilhardina* very well, and especially exhibits great resemblance to the Europe species *T. belgica*. But it is even more primitive than *T. belgica* by presenting equally developed p1/1 and p2/2, which are simplified in morphology and reduced in size, but loosely spaced and aligned in line. Consequently the material can be reasonably regarded as one of the most primitive euprimates.

Higher lever division of the order Primate from phyletic aspect is dichotomous: Strepsirhini and Haplorhini (Fleagle, 1999). But essential morphological differences between the two groups are scarce. We also undertake cladistic analysis using the data set published by Ross *et al.* (1998) with *Teilhardina* n. sp. added and some other modification to examine whether the new material will clarify the dichotomy of euprimates since their first appearance, or will narrow the gap between Strepsirhini and Haplorhini. Our results indicate that new material of *Teilhardina* from China does not fill the gap between strepsirhine and haplorhine and collapse the basal dichotomous structure of primate classification on higher level. This strengthens that dichotomous division of euprimates occurred since their appearance in the earliest Eocene.

The discovery of the most primitive omomyid euprimate material from China also indicates an Asian origin of omomyids with great possibility. Although the new material is not older than other earliest euprimates found in Euro-America, it is very near to the common ancestor of euprimates in morphology. The possibility of finding morphologically more generalized euprimates (or proto-euprimates) in southern China may not be dismissed.

Stratigraphy and geologic age of the primate-bearing Pondaung Formation at Paukkaung area, Myanmar

Maung Maung

Department of Geology, Mandalay University, Myanmar

Paukkaung area, in central Myanmar, is made up of fluvio-deltaic sediments encompassing the "Upper Member" of late middle Eocene Pondaung Formation. In general it occupies at the central part of a localized anticline, lying in the eastern limb of the Salin syncline. This area has four localities (Pk1, Pk2, Pk3, and Pk5) that produced invaluable primate fossils, and these fossils yielded from lower part of the "Upper Member" .

Myanmar-Japan Joint Pondaung Fossil Expedition Team has been studying the fossil mammals and stratigraphy of Pondaung area since 1998. During November of 2002, the team also carried out a paleontological investigation on primates and mammalian fauna from the Pondaung Formation in this area. In the field trip, a right maxillary fragment with M^{1-2} of *Pondaungia cotteri* was discovered at Pk5 locality (Ayoetawpontaung Kyitchaung). This locality is approximately 700 m far from Pk1 locality, where a postcranial specimen of a large primate was discovered (referred to *Pondaungia* by Ciochon et al., 2001).

Tsubamoto et al. (2002) have reported the fission-track zircon age of 37.2 ± 1.3 Ma from the tuff at the Pk1 locality, which is stratigraphically just 1 m above the horizon of the primate postcranial specimen. In addition, we discovered tuff bed also at the Pk5 locality, which is about 3.20 m above the new maxillary specimen. Therefore, the age of this *Pondaungia cotteri* is decided to 37.2 ± 1.3 Ma.

Moreover, Pk5 locality is about 1200 m and 1400 m far from Pk2 and Pk3 localities, respectively, where three primate taxa, *Amphipithecus*, *Pondaungia*, and *Eosimias*? (Pk2), and *Amphipithecus* (Pk3) have been discovered.

In conclusion, our detailed stratigraphic work at this area revealed that the primate fossil-bearing beds from Pk1, Pk2, Pk3, and Pk5 localities are almost similar in geologic age, lithology, sedimentology, and stratigraphic horizon.

The Pondaung primates in relationship to the faunal transition during the middle/late Eocene in East Asia

Masanaru Takai, Takehisa Tsubamoto, Naoko Egi, Nobuo Shigehara

Primate Research Institute, Kyoto University, Japan

The latest middle Eocene Pondaung fauna (central Myanmar) has been known for producing primate fossils since the beginning of the 20th century. To date four genera (*Pondaungia*, *Amphipithecus*, *Myanmarpithecus*, and *Bahinia*) have been discovered from the Pondaung fauna, and they are likely to be classified into two groups: Amphipithecidae (*Pondaungia*, *Amphipithecus*, and *Myanmarpithecus*) and Eosimiidae (*Bahinia* and unnamed new taxon), though the systematic positions of these two groups have not yet been settled down.

Amphipithecids are medium (*Myanmarpithecus*, 1.8 kg) or large (*Amphipithecus*, 6 kg; *Pondaungia*, 5.3-8.5 kg) size primates retaining relatively small premolars in respect to large molars. Although amphipithecids show some "anthropoid-like" features in dental and mandibular morphology, it is confirmed that the postorbital closure is not completed in *Amphipithecus*. Consequently, some researchers regard amphipithecids an adapoid (= adapiform) primates, which is closely related to notharctines, but the lower premolar morphology of amphipithecids is quite different from that of notharctine adapoids. Recent discoveries of the maxillary specimens of *Pondaungia* and *Amphipithecus* reveal that there is a considerable difference in the structure of the maxillary between *Pondaungia* and *Amphipithecus*.

On the other hand, eosimiids is much smaller primates (*Bahinia*, 0.75 kg) with relatively sharp cusps. Recently, a small calcaneus and mandibular fragments probably of eosimiids were discovered. The mandibular specimen is evidently larger than that of *Eosimias* from the middle Eocene of China, and smaller than that of *Bahinia*. This new mandibular specimen should be classified into a new taxon.

Besides eosimiids and amphipithecids, several Paleogene euprimates have been

discovered from many Eocene faunas in East Asia. We have analyzed such primate-producing faunas in comparison with other Eocene land mammal faunas in East Asia. The Pondaung fauna is most similar to the Naduo fauna (late Eocene) and Upper Lumeiyi fauna (middle Eocene) of southern China, neither of which contains primate fossils unfortunately, and is likely to be slightly younger than the latter and older than the former, respectively. The present fossil records suggest that the appearance of amphipithecids may be later than that of eosimiids, in East Asia. The discovery of amphipithecids from the Oligocene of Bugti, Pakistan, seems to support this view.

In addition, we have compared main 30 East Asian Eocene faunas, classifying them into three areas, northern, middle and southern areas. The conclusion of our analysis is as follows: (1) During the early middle and middle middle Eocene, most of entire East Asian faunas were very similar to one another. By the beginning of the late Eocene, the southern faunas differentiated from the northern faunas and each faunas became more endemic to one another. (2) The terrestrial "Eocene-Oligocene transition" in East Asia seems to have first begun in the southern part around the middle-late Eocene boundary or in the middle East Asia during the middle Eocene. The origin and evolution of eosimiids and amphipithecids should be discussed in relationship to these faunal transition during the later Eocene age.

The contribution of Thailand for the understanding of primate evolution in SE Asia

Yaowalak Chaimanee

Paleontology Section, Geological Survey Division, Department of Mineral Resources,, Thailand

Several groups of primates have been recovered in Thailand. An hoanghoniid adapiform had been described as *Wailekia orientale*, an oligopithecid anthropoid by Ducrocq et al. (1995) from the late Eocene of Krabi Basin, Penninsular Thailand. However, additional studies revealed its hoanghoniid affinities, which may represent a primitive sister group of the sivaladapids. Anthropoid is only represented by *Siamopithecus eocaenus* Chaimanee et al., 1997. However, its more primitive premolars structure, resembling that of *Bahinia*, exclude it from Amphipithecidae *senso stricto*, which include, *Myanmarpithecus, Amphipithecus* and *Pondaungia*. This crown group of Amphipithecidae can be characterized by the strong development of the metaconid and the extreme transverse elongation of the lower premolars. The resemblance between *Siamopithecus* and *Bahinia* premolars is based only on shared primitive premolars. The molars are very different, those of *Siamopithecus* bearing many similarities with those of the Amphipithecidae. However, *Bahinia* has a deep lower horizontal branch of the lower jaw, a character shared by all known Eocene Southeast Asian anthropoids. It is proposed therefore *Siamopithecus* in Siamopithecinae nov. sub-family. The anthropoid status of *Siamopithecus* has not been questioned, unlike that of the Amphipithecinae. However, it is clear that they belong to the same monophyletic Southeast Asian group, which occurs also in early Oligocene of Pakistan and that they therefore share many derived characters.

Tarsius thailandicus Ginsburg & Mein, 1987 has been discovered from an early Middle Miocene age of Li basin. It testifies the occurrence of *Tarsius* in Asia since the Middle Eocene (Beard, 1998). From this locality, the same authors reported the presence of a slow loris, *Nyctycebus linglom* Mein & Ginsburg, 1997. One isolated lower molar of hominoid has been originally described as *Dendropithecus orientalis* by Suteethorn et al. (1990) from

Middle Miocene of Ban San Klang locality. However, the reanalysis of this fossil by Harrison & Gu (1999) lead to its attribution to pliopithecids. Plio-Pleistocene deposits in Thailand are largely distributed around the country. Cercopithecoidea are the most abundant primates in Plio-Pleistocene localities. Their appearance in Thailand can be bracketed between the Middle Miocene and the Late Pliocene. *Pongo* teeth are also rather common in late Middle Pleistocene. Age and place of origin of that modern ape is still unknown, but the Southeast Asian origin is more than probable, according to its Plio-Pleistocene range. *Homo* remains are scarce and mostly limited to Holocene, associated with archaeological sites. However, an isolated tooth of *Homo* sp. from a late Middle Pleistocene cave deposit in NE Thailand was described by Tougard et al. (1998). Recently, a skull fragment of cf. *Homo erectus* has been discovered from Northern Thailand. Its associated mammal fauna suggests a late Middle Pleistocene age.

To conclude, it appears that Thailand has now a high potential for the study of origin and evolution of Primates. All major groups are documented, from their origin to the differenciation of man. Future discoveries will demonstrate that Southeast Asia has played a more critical and more important role for primate evolution as presently expected, almost as important as that of Africa. Many faunal exchanges, so far not well documented, must have occurred between these two primate evolutionary centers during the Tertiary, making the reconstruction of primate evolution much more complicated than previously expected, in regard of the "All African Model" of primate evolution.

The importance of South Asia in the evoluton of anthropoid primates

J.-J. Jaeger

Institut des Sciences de l'Evolution, Université Montpellier II, CC 064-Palace E. Bataillon, 34095-Montpellier Cedex 05, France

New Middle Eocene primates and afrotheres from northwestern Africa and their contribution to the understanding of African-Asian faunal exchanges

Rodolphe TABUCE

Institut des Sciences de l'Evolution, Université Montpellier II, CC 064-Palace E. Bataillon, 34095-Montpellier Cedex 05, France

The study of several new taxa, including some primates, from the Algerian localities of Glib Zegdou (early to middle Eocene) and Bir El Ater (late middle Eocene) allows me to discuss the African-Asian faunal exchanges during the Eocene and to analyze if the latter are compatible with the recent discoveries and advances concerning the basal phylogeny of anthropoid primates.

At present, the oldest African anthropoid is *Algeripithecus* from the Glib Zegdou. New primates from Bir El Ater document two Paleogene typical African groups: new specimens of *Biretia* demonstrate its affinities with *Algeripithecus* within the qatraniine "parapithecids", and an oligopithecid -the earliest representative of this family- is reminiscent of the Asian eosimiid *Bahinia*. In order to infer the possible relationships that might have existed between these primates, we performed a phylogenetic analysis including most recent data on Asian and African primates. The results reveal dental convergences between oligopithecids and eosimiids, and it appears that a radiation of small bunodont forms (*Altiatlasius* included) occurred in Africa during the early Paleogene. The occurrence of anthropoids in the early to middle Eocene of Africa (e.g. *Algeripithecus*) and in the middle Eocene of Asia (*Eosimias* and *Bahinia*) suggests a faunal interchange between both continents during the early Eocene. However, two problems need to be addressed: (1) the morphological gap between these anthropoid groups seem to indicate an earliest migration (?Paleocene); the hypothesis of an ante-Ypresian origin for the anthropoids is supported by our suggestion to incorporate *Altiatlasius* within the Tarsiidae-Anthropoidea clade. (2) No other fossil documents such an exchange. All known mammalian migrations at this period concerning Africa seem to imply only Europe, and the new currently studied taxa (elephant-shrews,

condylarths, batsÉm) reinforce this opinion. Consequently it is difficult to demonstrate with the current fossil record an early Eocene migration of anthropoids from Asia towards Africa.

During the middle Eocene, a mammalian exchange between these two continents is more evident and adequate to discuss another Paleogene primate event: the origin of Catarrhini. This group included then the Propliopithecidae from the early Oligocene of Fayum and Oman, and putatively the Amphipithecidae from the Eocene of Myanmar and Thailand. The origin of this clade is unknown. According to the current data, we can assume an Eocene African endemism of "parapithecids" and, subsequently, a middle Eocene immigration of catarrhines in Africa from Asia. As a matter of fact, the anthracotheriid artiodactyls from the Fayum have their origin in South-East Asia and the discovery of an undetermined anthracothere at Bir El Ater corroborates a middle Eocene migration for these mammals. Moreover, the same locality has yielded two rodent families which are undoubtedly related to South-East Asian Eocene groups. Thus, a middle Eocene immigration of catarrhines in Africa from Asia is likely. However, the combined absence of propliopithecids both at Bir El Ater and in the lower sequence of the Fayum seems sufficient to exclude this assumption. As suggested by some authors, the emergence of propliopithecids in the upper sequence of Fayum would not testify to an Asian immigration but to an evolution of the African primate communities (modification of the trophic structure) around the Eocene-Oligocene boundary.

The adaptations of Pondaungia and Amphipithecus, South Asian late Eocene primate

Richard F. Kay, Daniel Schmitt, Christopher Vinyard, Nobuo Shigehara, Masanaru Takai

Dept. of Biological Anthropology and Anatomy, Duke University Medical Center, U.S.A.

Our analysis of recently reported finds of upper and lower teeth and mandibular, humeral, and calcaneal fragments indicate that the Amphipithecidae (*Pondaungia* and *Amphipithecus*) (late middle Eocene, Myanmar) were a slow moving quadrupedal seed predator.

At 5-6 kg, these taxa is as large as any known Eocene primate, and comparable in size to the largest extant platyrrhines and strepsirrhines. The mandibular corpus of both taxa is robust and the symphysis is rugose with strong transverse tori, both suggesting an ability to resist large chewing loads. The robust spatulate upper central incisor and projecting robust upper canine of *Pondaungia* indicate powerful biting as occurs in husking. The molars of *Amphipithecus* and *Pondaungia* have weak shearing crests and narrow occlusal surfaces. These features and thick enamel with a preponderance of microwear pits, suggest a hard-object, low-fiber diet. Collectively, the dental and mandibular anatomy suggests these large-bodied amphipithecids were a seed predators.

Postcranial bones (humerus, ulna, and calcaneus) of a single individual have been attributed to *Pondaungia* but they are not associated with dental material of that taxon and could equally belong to *Amphipithecus*. The humeral head is rounded and proximally oriented with low tuberosities indicting an extremely mobile shoulder like that of living lorises and *Alouatta*. The elbow joint exhibits articular features for enhanced stability in habitually flexed positions: a screw-type trochlea, an anteriorly expanded capitulum, and an expanded grooved capitular tail. These distal humeral features, along with a large medial epicondyle, are shared with Alouatta, a slow moving quadruped. The distal humerus of deliberate arboreal quadrupedal lorids is less similar-- the enlarged capitulum and capitular tail are the only features in the above list common to both. The short distal load arm of the calcaneus also is consistent with, but not exclusive to slow arboreal quadrupedalism.

Discovery of a new clade of Asian Primates from the late Eocene of the Baise Basin (Guangxi Zhuang Autonomous Region, People's Republic of China): The impact of global climate change onpPrimate phylogeny and biogeography

K. Christopher Beard[1], Qi Tao[2], Guo Jianwei[2], and Daniel L. Gebo[3]

[1]Section of Vertebrate Paleontology, Carnegie Museum of Natural History

[2]Institute of Vertebrate Paleontology & Paleoanthropology, Chinese Academy of Sciences

[3]Department of Anthropology, Northern Illinois University

Ekgmowechashala philotau is an enigmatic fossil mammal from the early Arikareean (late Oligocene) of South Dakota and Oregon, USA. Traditionally interpreted as an omomyid primate, the phylogenetic position of *Ekgmowechashala* remains contentious. McKenna (1990: *Geological Society of America Special Paper* **243**: 211-234) views *Ekgmowechashala* as a derived member of the Plagiomenidae, an extinct group of placental mammals that is often allied with Dermoptera. Both omomyids and plagiomenids are well documented in Eocene strata in North America. Under either of these phylogenetic reconstructions, *Ekgmowechashala* plausibly evolved in situ in North America, with a ghost lineage spanning most of the Oligocene.

However, neither of these competing phylogenetic reconstructions is consistent with current knowledge of the anatomy of *Ekgmowechashala*. For example, the hypothesis that *Ekgmowechashala* is an omomyid primate suffers from the fact that *Ekgmowechashala* retains a double-rooted p2. Among Primates, a double-rooted p2 occurs only in certain adapiforms (e.g., *Cantius*, *Notharctus*, *Hoanghonius*, *Europolemur*) and stem primate taxa such as *Altanius orlovi* from the Bumbanian of Mongolia. Significantly, no living or fossil haplorhine is known to have retained this primate plesiomorphy. Both *Teilhardina* and *Steinius* (the earliest and most primitive omomyids known to date) possess a single-rooted p2. The same condition holds in tarsiids and those anthropoids that retain p2. Because this character transformation is an unlikely candidate for reversal, the hypothesis that *Ekgmowechashala* is an omomyid is difficult to reconcile with its p2 anatomy.

Similarly, McKenna's attribution of *Ekgmowechashala* to the Plagiomenidae is based in part on his unorthodox interpretation of its upper molar cusp homologies. The large buccal molar cusps that were initially regarded as paracone and metacone by Rose and Rensberger (1983: *Folia Primatologica* **41**: 102-111) were considered to be stylar cusps by McKenna. Smaller and more lingual structures that were interpreted as paraconule and metaconule by Rose and Rensberger were thought to be paracone and metacone by McKenna. To the extent that it is extremely rare among mammals for upper molar stylar cusps to be significantly larger and more voluminous than the paracone and metacone, the hypothesis that *Ekgmowechashala* is a plagiomenid is also questionable.

Joint expeditions by the Carnegie Museum of Natural History and the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences) have recovered the first *Ekgmowechashala*-like fossils outside of North America. The specimens were collected from a small outcrop of the late Eocene Naduo Formation in the Baise Basin, Guangxi Zhuang Autonomous Region, China. Their age, anatomy, and provenance imply a very different hypothesis for the evolutionary history of *Ekgmowechashala*.

Lower molar morphology in the Baise Basin specimens resembles that of *Ekgmowechashala* in remarkable detail. Both taxa possess bunodont lower molars with crenulated enamel. Lower molar trigonids are mesiodistally compressed, and the paraconids are reduced or absent. In the Baise Basin specimens, two large neomorphic cusps are evident on the distal side of the trigonid wall (or postvallid). The more lingual of these is a metastylid, which also occurs in *Ekgmowechashala*. A more buccally situated neomorphic cusp lies midway between the protoconid and metaconid on the postvallid. The latter cusp is not apparent in available specimens of *Ekgmowechashala*.

A maxillary fragment from the Baise Basin preserves M2 in good condition. In this specimen the two large buccal cusps are obviously the paracone and metacone, rather than enlarged stylar cusps. The protocone bears a well-developed postprotocingulum (or "*Nannopithex*-fold"). Both of these upper molar characters suggest that the Baise Basin taxon is a primate. At the same time, these characters conflict with possible plagiomenid affinities for *Ekgmowechashala* and its close Chinese relative.

The close correspondence in dental morphology between the Baise Basin primate and *Ekgmowechashala* leaves little doubt that the two taxa are closely related. Here, both are referred to the primate family Ekgmowechashalidae. The broader affinities of Ekgmowechashalidae with other primates are difficult to reconstruct at present. The presence of a double-rooted p2 renders any close relationship with Omomyidae (or other haplorhines) doubtful. On the other hand, shared derived characters that might link Ekgmowechashalidae with adapiforms are not readily apparent. For the moment, Ekgmowechashalidae can be regarded as a very basal clade of primates whose exact phylogenetic position within the order is unclear.

The discovery of an early relative of *Ekgmowechashala* in Asia requires a fresh look at the historical biogeography of this primate clade. As noted above, previous workers have generally regarded *Ekgmowechashala* as evolving locally in North America from geologically older omomyid or plagiomenid ancestors. Our new evidence suggests instead that *Ekgmowechashala* dispersed from Asia to North America across the Bering land bridge during the late Oligocene, coincident with a short but pronounced warming trend that saw global mean annual temperatures rise by about 4-5° Celsius. If our revised biogeographic hypothesis is correct, the history of primates in North America is marked by successive immigration from Asia, followed by continental-scale extinction. The first of these episodes occurred at the beginning of the Eocene, when basal adapiform (*Cantius*) and omomyid (*Teilhardina*) primates dispersed to North America from Asia. This initial primate colonization of North America coincided with dramatic global warming at the Paleocene-Eocene boundary. By the end of the Eocene, North American primates were extinct—apparently as a result of long-term climatic deterioration. The second bout of primate colonization of North America consisted of the dispersal and subsequent extinction of *Ekgmowechashala*. The Quaternary dispersal of *Homo*, presumably along the same route utilized by early Eocene primates and *Ekgmowechashala*, stands as the third such iteration.

The zoogeographic and phylogenetic relationships of early catarrhine primates in Asia

Terry Harrison

Department of Anthropology, New York University, 25 Waverly Place, New York, NY 10003, USA

Catarrhines originated in Afro-Arabia during the Paleogene, and were restricted to this zoogeographic province until the early Miocene. During this period of isolation, several major clades of catarrhines originated, including the propliopithecids, pliopithecids, proconsulids, dendropithecids, cercopithecids and hominoids. The earliest members of the Catarrhini, the Propliopithecidae, are known from early Oligocene localities in Egypt, Oman, and possibly Angola. Unfortunately, the fossil record for catarrhine evolution in Africa is poorly documented for much of the Oligocene, with a 10 million year gap in the fossil record. It is during this temporal hiatus that the pliopithecids presumably diverged, although their occurrence in Africa is entirely unknown. The pliopithecids are primitive catarrhines with a wide geographical distribution throughout much of Eurasia during the Miocene. They are the earliest catarrhines to migrate out of Africa at ~20-18 Ma. Proconsulids and dendropithecids are basal catarrhines of modern aspect from the late Oligocene to mid-Miocene of East Africa. Although they are the most taxonomically and adaptively diverse groups of catarrhines during the Miocene, they were probably restricted to Africa (although some Eurasian taxa have been phyletically linked with them in the past). It may well be that their specialized morphology and relatively narrow niches limited their ability to extend their geographic range. This hypothesis is supported by evidence of marked zoogeographic provinciality in East Africa during the early Miocene. Crown catarrhines belonging to Hominoidea and Cercopithecoidea appear to have originated in Africa prior to 20 Ma, but neither clade becomes an important component of the catarrhine fauna until the middle Miocene (~16 Ma), and even then their taxonomic diversity remains low. During MN 5 and basal MN 6 (~17-15 Ma) hominoids expanded into Europe, soon after the arrival of pliopithecids. The first record of cercopithecids in Eurasia is much later (MN 9, ~11-9 Ma).

The earliest known catarrhines in Eurasia are from the Xiaocaowan Formation, Sihong, China (correlating with MN 4, ~18-17 Ma) belonging to *Dionysopithecus* and *Platodontopithecus*. These dionysopithecines represent the primitive sister-group of all other pliopithecids, and suggests that European representatives of the clade (which make their first appearance during MN 5 at ~17-16 Ma) may have been derived from an Asian source. Dionysopithecines probably entered tropical and subtropical Asia from Africa during MN 3 (~20-18 Ma), and diversified locally. From this source, a more specialized group originated in East Asia, the pliopithecins, represented by *Pliopithecus zhanxiangi* from Tongxin in China (MN 6, ~15 Ma), and they extended their range westwards into Europe by ~17-16 Ma. The specialized crouzeliins appear, however, to have originated in Europe from a pliopithecin-like ancestor, where they are first recorded at localities corresponding with MN 6. The only known crouzeliin from Asia, *Laccopithecus*, from the late Miocene (~7-8 Ma) of Shihuiba, China, points to a late arrival of this clade into the region. Moreover, the extinction of pliopithecids in Europe by the close of the Vallesian would indicate that late surviving crouzeliins reached Asia before ~11 Ma, possible at the same time as hominoids.

Other early catarrhines from Asia, such as those from Ertemte and Taben-Buluk in China, Haritalyangar in India, and the Kamlial and Manchar Formations in Pakistan, are too poorly known to determine their phylogenetic affinities. The specimens from the early Middle Miocene of Pakistan (~17-16 Ma) are probably not closely related to the pliopithecids, and may have closer ties with dendropithecids or proconsulids. The same can be said for important undescribed fossil catarrhines collected by Dr. Jin Changzhu at the middle Miocene locality of Fanchang in Anhui Province, China. Finally, an isolated molar from Ban San Klang in northern Thailand (~17-15 Ma), originally described as *Dendropithecus orientalis*, is provisionally recognized as belonging to a species of *Dionysopithecus*.

Important discoveries of fossil primates have been made in China and Southeast Asia in the past decade that have added significantly to our appreciation of the zoogeographic and phylogenetic relationships of early catarrhine primates. It is clear from these findings, however, that we have sampled only a fraction of the taxonomic diversity that occurred in this region during the Miocene and Pliocene. Without a better representation of these taxa in

time and space it will prove exceedingly difficult to realistically reconstruct the zoogeography of Asian primates.

New material of small-sized primates from the Late Miocene of the Yuanmou, Yunnan

Pan Yuerong

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences

The Xiaohe-Zhupeng, Leilao hominoid localities are situated at the northwest part of the Yuanmou basin. It is famed for its numerous remains of the large hominoid primate, *Lufengpithecus yuanmouensis*. In fact, there are three smaller primates besides the *L. yuanmouensis,* which are a new small-sized ape and *Sinoadapis* sp. nov as well as *Indraloris* sp. nov, which is first reported in China.

Both the dental morphology and size of the small ape are different from those of the *Laccopithecus robustus* from Lufeng. The size of which is smaller than that of *Laccopithecus* and is relatively similar to small apes from East Africa and south Asia, in morphology. It differs from Pliopithecidae in that the m1 and m2 are suboval in occlusal outline, the 5 cusps of the lower molars are relatively round well-defined groove between each of the main cusps and is placed the margin of the crown so that the talonid basin is larger. The mesial fovea is transversely wide. The protoconid and metaconid are compressed anteroposterioly and much placed in the mesial part of the crown. The hypoconulid is developed. Moreover, there are no pliopithecine triangle in the talonid basin and waisting on the buccal side of the crown. The upper molars are relatively round in outline.

The discovery of the small ape from Yuanmou provides a new information for gibbon origin. It suggests that the small ape might be immigrated from East Africa via south Asia into Yuanmou.

The *Sinoadapis* sp. nov is different from the *Sinoadapis* from Lufeng in the smaller size, the mesial arm of the hypoconid extends more internally in the lower molar. The mesial basin is small and shallow. The cusps is sharper. *Indraloris* sp. nov is distinguished from *Indraloris himalayensis* in dramatic reduction of the entoconid, the hypoconulid is much developed.

The Primate combination of the Yuanmou is corresponding to that of Haritalyangar in India which contain *Sivapithecus sivalensis*, *Krishnopithecus krishnaii*, *Sivaladapis nagrii* and *Indraloris himalayensis*, so the geological age of the Yuanmou hominoid locality may be 9 Ma.

East is east and west is west: Relations among European and Asian Miocene hominids

D.R. Begun

Department of Anthropology, University of Toronto, Toronto, ON M5S 3G3, Canada

For much of the 20th century the large bodied fossil great apes of Eurasia were considered to be closely related to each other and to living great apes. Most Eurasian fossil great apes were at one time or another assigned to the genus *Dryopithecus*. Today there are at least 7 widely recognized genera of Eurasian fossil great apes, the relations among which, and with living great apes, are unresolved. Here I make a case for the existence of two main hominid clades in Eurasia, an eastern clade most closely related to living orang-utans and a western clade most closely related to living African apes. The relationship between Asian fossil and living great apes is generally recognized, but that between European and African great apes is more controversial. I focus therefore on the evidence for a specific relationship between *Dryopithecus* and *Ouranopithecus* on the one hand and African apes and humans on the other. Cranial and postcranial synapomorphies support this hypothesis, as does the paleobiogeography of a number of late Miocene mammal lineages. The eastern and western clades of the Hominidae appear to have originated in the circum-Mediterranean region from a *Griphopithecus-like* ancestor.

Postcranial fossils of *Ankarapithecus meteai* and the evolution of hominoid locomotion.

B.G. Richmond[1], J. Kappelman, and M. Maga

[1]Department of Anthropology, George Washington University 2110 G St, NW, Washington, DC 20052, U.S.A.

One of the central questions concerning hominoid evolution is whether or not similarities in the postcranial skeletons of modern great apes and humans, and extant hominoids more generally, are homologous or the result of independent evolution. Recently recovered postcranial fossils attributable to *Ankarapithecus meteai* are relevant to this debate. A largely complete right radius and fragments of two manual phalanges (proximal and middle) were recovered in 1995 in the same locality (12) that yielded a partial skull (AS95-500) and a partial face (MTA 2125, found in 1967 by Ozansoy) of *A. meteai*. Measurements of these fossils were compared to an anthropoid sample (*Pan*, *Pongo*, *Papio*, *Alouatta*, and *Presbytis*) with diverse locomotor adaptations. The radius resembles those of extant hominoids in some ways, including having a deep capitular fossa, a bevel on the side of the head (suggesting a well-developed zona conoidea on the humerus) and a more rounded head compared to nonhominoid anthropoids. In other respects, the radius resembles extant pronograde arboreal and terrestrial quadrupeds, including a strongly tilted head, a short radial neck, and a very sharp interosseous crest. The proximal phalanx fragment lacks strongly developed flexor ridges, and is only slightly curved. Taken together, the morphology indicates that the forelimb of *A. meteai* lacked the suspensory specializations of extant apes, and instead typically used pronated hand postures, probably in terrestrial and arboreal settings. The preserved anatomy of *A. meteai* suggests a stronger terrestrial component than appears to have been the case for *Sivapithecus*. These fossils support the hypothesis that substantial levels of homoplasy occurred in the evolution of hominoid locomotor skeleton.

Evolution and extinction of Siwalik fossil apes: A review based on new palaeoecological and palaeoclimatological data

Rajeev Patnaik[1] and David Cameron[2]

[1]Center of Advanced Study in Geology, Panjab University

[2]Department of Anatomy and Histology, The University of Sydney

Tibetan-Himalayan uplift models, carbon and oxygen isotopes from pedogenic carbonates, endemic upwelling of planktonic foraminifers and palynological data, all point towards a possible intensification of monsoons and a marked ecological shift in the Late Miocene (between 8-7 Ma) in South Asia. In the Siwalik deposits, a dramatic change in the diversity of muroid rodents (from cricetid dominated to murid dominated) around this time (8-7 Ma) has also been observed. This replacement of cricetids by murids in the Late Miocene time can be attributed to an intensification of monsoon system, as most of the present day murids are found in the monsoon affected region of the world and their reproduction-oriented life history strategy is better suited to unpredictable and seasonal climatic conditions. Also, it has been found that, within murids, a remarkable increase in the size of their first upper molars (reflecting increase in body size) and grazing behavior, coincides with the spread of warm season grasslands in the Indian subcontinent.

The Late Miocene tropical grasslands spread from Africa in the west to the Indian subcontinent in the east (Retallack, 1991). Within the Indian subcontinent a difference in timing of the C3-C4 ecological shift has been observed. In the Potwar area, Pakistan, it was at about 8.8-8.6 Ma, in Surai Khola, Western Nepal it was about 7.4 Ma (Cande and Kent, 1992, time scale) and in Bakia Khola in Central Nepal it was at about 6.6 or 5.9 Ma (Harrison, et al., 1993; Quade et al., 1995). The Miocene ape *Sivapithecus* disappeared from Pakistan by 8.5 Ma, but in India (Haritalyangar) it persisted till 8 Ma and *Gigantopithecus* (*Indopithecus*) survived till 7.3 Ma (Johnson et al., 1983 dates readjusted after Cande and Kent, 1992). This also could have happened because of the destruction of the forest habitat preferred by apes by encroaching grasslands at a later stage in India. In the Pliocene, desert

also spread from Africa in the west to India in the east (Retallack, 1991).

This paper also re-examines the taxonomic status of the Siwalik hominid traditionally allocated to *"Gigantopithecus"*. It is argued here that this hominid should be reallocated to *Indopithecus* Pilgrim, 1915. This conclusion is based on differential patterns of mandibular and dental morphology observed between these taxa. It is also suggested that any similarities between these taxa is a result of functional convergence. They are sufficiently different in their morphology and by inference their modes of mastication to be considered generically distinct. The phylogenetic significance of these hominids remains obscure as mandibular form is largely the result of function, rather than phylogenetic history.

Late Miocene Asian hominoids and orangutan ancestry

J. Kelley

University of Illinois, Chicago, U.S.A.

Overall, the orangutan arguably has the most derived morphology among extant great apes. Knowing the evolutionary history of the orangutan is important not only for understanding the derivation of its unusual morphology, but also for addressing broader questions, such as whether the extant ape body plan is shared from the last common ancestor of the group or has been independently derived in Asian and African clades.

Most Asian fossil hominoids are now generally regarded as being within the orangutan clade, although this is not universally accepted. Even if this is so, none of the relevant taxa presents an overall morphological pattern that suggests a particularly close relationship to the living orangutan. Species of *Sivapithecus* from South Asia share a number of apparently derived cranial features with *Pongo*, although whether all of these are truly synapomorphies has been questioned recently based on a new early cercopithecoid cranium from Kenya. Moreover, *Sivapithecus* does not possess the derived dental features of the orangutan, and, in its known postcranial anatomy, shares few if any likely orangutan synapomorphies. *Lufengpithecus lufengensis* from southern China also shares several purported cranial and dental synapomorphies with *Pongo*, most of which are different features than those shared by *Sivapithecus* and *Pongo*. However, in those cranial features that most clearly distinguish *Pongo* from other apes, *L. lufengensis* does not appear to closely resemble *Pongo*, or the morphology is too distorted to permit a definitive character assessment. *L. lufengensis* also possesses a suite of apparent apomorphic features that could be interpreted as precluding it from direct orangutan ancestry.

Among newly described fossils from the Yuanmou Basin, also in southern China, is a largely undistorted infant cranium, assigned to *Lufengpithecus hudienensis*. The preservation of this specimen affords an opportunity to evaluate cranial morphology that is poorly or insufficiently preserved in *L. lufengensis*. Comparison of the infant cranium to

equivalently aged crania of extant great apes reveals an overall morphological pattern that is broadly similar to that of *Pan*, with few if any features that can be viewed as plausible synapomorphies of *Pongo*.

Thus, in spite of a growing late Miocene Asian fossil hominoid record, orangutan ancestry remains obscure, as does the history of its morphological evolution.

The preferred habitats of *Sivapithecus* and paleoenviromental changes leading to its extinction in the Siwaliks of Pakistan

Sherry Nelson

University of Michigan, Ann Arbor, U.S.A.

The Siwalik sediments of Pakistan, spanning the past twenty million years, offer the only nearly continuous record of faunal and environmental change documenting an ape clade throughout its evolution and demise. Within this sequence, *Sivapithecus* appears around 13 Ma and disappears at 8.4 Ma. The purpose of this investigation is to determine the preferred habitats of *Sivapithecus* and whether changes in habitat or climate may have led to its extinction. Inferences are drawn from the following three studies: 1) an analysis of dental microwear to determine the preferred diet of *Sivapithecus*, fruit availability in its habitat, and changes in fruit availability that might have led to its extinction; 2) an isotopic study of tooth enamel from two time intervals to reconstruct the vegetation mosaic when *Sivapithecus* was present and shortly after it went extinct in order to determine what *Sivapithecus* habitat was like and what changes in habitat and climate may have taken place by the time it went extinct; and 3) a study of intra-tooth isotopic variability in equid teeth to determine whether *Sivapithecus* habitats were characterized by a seasonal rainfall regime, and if so, what kind of forest is associated with that regime and what changes in climate may have occurred by the time *Sivapithecus* went extinct.

A new method of dental microwear analysis is presented in which features are examined under a light microscope, and results are analyzed using a Bayesian general location model. Interpreting diets in terms of Bayesian posterior probabilities relative to multiple known modern diets permits the possibility that there is no perfect modern analogue. Furthermore, species' diets are reconstructed in terms of relative proportions of different food categories, thus allowing changes in proportions to be tracked over time in order to infer changes in fruit availability. These analyses indicate that a range of Siwalik fauna, including *Sivapithecus*, were as frugivorous as their modern rainforest counterparts.

Sivapithecus habitat preference was therefore probably similar to that of modern apes in fruit abundance. The extinction of *Sivapithecus* and two frugivorous tragulids around 8.6-8.4 Ma, combined with shifts from fruit to browse in some small bovids, and shifts from browse to graze in larger bovids, suggests replacement of forest by open habitat, accompanied by a decrease in fruit availability. Continual presence of frugivorous suids and very small bovids, however, suggests that some forest was still present well after the extinction of *Sivapithecus*.

Isotopic evidence indicates that the Siwaliks were characterized by a vegetation mosaic of forest, woodland, and open habitats as early as 9.3 Ma. By 8.1 Ma, much of the forest was replaced, but not completely eliminated, by more open habitat, including patches of C_4 grass. This vegetation mosaic supported fauna, which exploited a range of habitats. Many of these species go extinct over the time interval sampled, with species most dependent on closed habitat or fruit going extinct first. The pattern of extinctions combined with vegetation mosaic reconstructions suggests fragmentation and loss of forest over time, leading to frugivore extinctions, including *Sivapithecus*.

Isotopic reconstructions of the precipitation regime from 10.0 to 6.3 Ma are similar in seasonality to those experienced in southern China today. These reconstructions suggest a dry season of 5-6 months, with an intense rainy season. The Asian monsoon was therefore most likely established by 10 Ma. Amount of annual rainfall decreases over time and likely resulted in a shift from wet monsoon forests to dry monsoon forests, with the first phase of this shift occurring around the time *Sivapithecus* went extinct.

Combined isotopic evidence of the vegetation mosaic and seasonal precipitation regime suggests *Sivapithecus'* habitat was most similar to monsoonal forests today, with a shift from wet monsoonal to dry monsoonal forests from 10 to 6.3 Ma. Monsoonal forests do not support great apes today, but there is no current evidence that *Sivapithecus* might have differed in habitat and dietary requirements from those of extant great apes. Microwear analyses indicate that many species, including *Sivapithecus*, were as highly dependent on fruit as their modern rainforest counterparts. Thus *Sivapithecus* appears to have inhabited a forest more seasonal than those great apes inhabit today, but a forest that was probably similar to modern ape habitat in terms of the spatio-temporal availability of fruit. This forest was

replaced by more open habitat over time as amount of annual rainfall decreased, resulting in the extinction of many frugivores, including *Sivapithecus*.

The comparisons of tooth size and morphology between the late Miocene hominoids from Lufeng and Yuanmou, and the implications for their diet, behavior and environment

LIU Wu[1] and ZHENG Liang[2]

[1]Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences

[2]Provincial Institute of Archaeology, Kunming

Late Miocene hominoids from Lufeng and Yuanmou of Yunnan Province in south China are among the most prolific fossil hominoids in Eurasia. The two sites are very close from each other with nearly the same ages. In the past 10 years, comparative studies of cranial and dental morphology, metric and morphometric analyses between *Lufengpithecus lufengensis* and Yuanmou hominoids indicate that the two hominoid assemblages resemble each other more than each of them with other Miocene hominoids around the world. So, some colleagues have proposed the two hominoids be put into the same genus with just species level differences. However, there are still some obvious shape, size and microstructure differences between *Lufengpithecus lufengensis* and Yuanmou hominoids. Recently, the comparisons of tooth size proportions, lower molar shearing crest development, tooth enamel thickness, body weight and tooth wear differences between *Lufengpithecus lufengensis* and Yuanmou hominoids were carried out trying to infer the diets and possible behavior, health condition, population structure and environment differences for the two hominoids. Our results show that *Lufengpithecus lufengensis* had relatively smaller front teeth, relatively smaller M^1, higher SQ than Yuanmou hominoids indicating that more folivorous and soft dietary items like leaves and berries were consumed. The tooth wear analysis further indicate that both upper and lower molars of the Yuanmou hominoids were more heavily worn than those of *Lufengpithecus lufengensis*. The tooth wearing patterns of the Yuanmou hominoid and *Lufengpithecus lufengensis* also exhibit some differences. The heaviest wears of lower molars of the Yuanmou hominoid occur in M_2, followed by M_1 and M_3. In *Lufengpithecus lufengensis*, the M_1 and M_3 were more heavily worn than M_2. Based on these findings, we

propose that except for the diets, all these differences may be also related to the possible influences of living environment, behavior pattern, population structure of the Yuanmou hominoid and *Lufengpithecus lufengensis*.

Study on enamel microstructure of Late Miocene hominoids from Yunnan of China

ZHAO Lingxia

Institute of Vertebrate Paleontology & Paleoanthropolgy, Chinese Academy of Science, Beijing

Late Miocene hominoid fossils found in Yunnan, China, are of great importance in exploring early hominid origin and hominoid phylogeny. Multidisciplinary studies on Yunnan hominoid fossils are helpful and necessary to understand its ontogeny and phylogeny. Preliminary study on enamel microstructure of lower permanent incisors of Yunnan Late Miocene hominoids was conducted using the Scanning Electron Microscope (SEM). The results show as following.

Perikymata are good recordings of the crown formation and the pattern of perikymata compactness can reflect the extension pattern of crown formation. The buccal surfaces of 6 Yunnan hominioid lower incisors show clear perikymata. The progressive narrowing of perikymata spacing from the incisal edge to the cervix indicates progressive slowing of crown extension rates. This characteristic of the enamel development in the Yuanmou hominoids is similar to that of *Lufengpithecus lufengensis*. Both of them are similar to *Australopithecus afarensis*, and different from robust *Australopithecus* which have relatively linear crown extention rates and do not show a distinct reduction of perikymata spacing at the cervix.

Periodicity of perikymata. Yuanmou hominoid YV2013 shows a 9-day periodicity of perikymata by longitudinal section, the same as one canine of *Lufengpithecus lufengensis*. The 9-day perikymata periodicities of the Yuanmou and Lufeng hominoids are within the variation of extant great apes and modern humans (6-11 days, mean 7-9 days); in contrast, monkeys and gibbons have shorter perikymata periodicities about 4-5 days, and Early Miocene *Proconsul* from Africa has a shorter perikymata periodicity 5-6 days. Thus this characteristic may reflect synapormorphies of dental development in the Yuanmou and Lufeng hominoids.

Estimation of crown formation times Refering to the perikymata periodicity and the cusp formation time (about 6 months), the crown formation times of the Yuanmou hominoid lower incisors are estimated. The mean perikymata number of the 4 Yuanmou hominoid lower incisors is 175 (range 163-191), which is greater than the Lufeng lower incisor PA895 (128 perikymata). Assuming the perikymata peroidicity is 7 or 9 days long, the mean estimated crown formation time of incisors is 3.9 or 4.8 years for the Yuanmou hominoids and 3.0 or 3.7 years for the Lufeng hominoids. Therefore the crown formation time of the Yuanmou hominoid incisors is nearly one year longer than that of Lufeng hominoids. Relating the crown formation time to the crown height measurements of incisors, the enamel extension rates of the Yuanmou incisors (with shorter crowns) are somewhat slower than those of the Lufeng teeth (with higher crowns).

Compared with the incisor crown formation times of Early Miocene *Proconsul* (2.0 years or so), those of the Late Miocene Yuanmou hominoid are more than a year longer. They are also longer than Plio-Pleistocene *Australopithecus afarensis* (mean 3.4 years of 4 incisors) and robust *Australopithecus* (mean 1.8 years of 5 incisors). However, the crown formation times of the Yuanmou hominoid incisors are closer to those of modern humans and extant great apes. The trait of longer dental growth processes may also reflect synapomorphies in hominoid evolution.

In conclusion, analysis on **dental development** of fossil hominoids can provide important information on ontogeny. The present study indicates incisor crown formation times of Late Miocene Yuanmou and Lufeng hominoids are closest to those of modern humans and extant great apes.

Hominoid fossils discovered from Chiang Muan, northern Thailand: The first step towards the understanding of the hominoid evolution in the Neogene Southeast Asia

Yutaka Kunimatsu[1], Benjavun Ratanasthien[2], Hideo Nakaya[3], Haruo Saegusa[4] & Shinji Nagaoka[5]

[1]Primate Research Institute, Kyoto University, Japan

[2]Chiang Mai University, Chiang Mai, Thailand

[3]Kagawa University, Takamatsu, Japan

[4]Himeji Institute of Technology, Sanda, Japan

[5]Nagasaki University, Nagasaki, Japan

After the end of the Early Miocene, hominoid primates expanded their distribution from Africa into Eurasia. In Western Eurasia (Europe - Anatolia), various fossil hominoids have been reported mainly from the Middle and Late Miocene. In Eastern Eurasia, the majority of Miocene hominoid fossils have been discovered from two areas: Siwaliks in Indo-Pakistan and Yunnan Province in southwestern China. These areas have yielded *Sivapithecus* (with very few specimens assigned to *Gigantopithecus*) and *Lufengpithecus*, respectively. In other parts of Eastern Eurasia, no Neogene hominoids have been known except for a single upper molar from Tinau Khola in Nepal and a relatively small and damaged mandible from Wudu in Gansu Province, China. While Southeast Asia is the homeland for extant Asian hominoids (orangutans and gibbons), we know almost nothing about the evolutionary history of hominoids in this region.

Recently, we started a paleontological and geological field survey in Thailand. Our purpose is to study the Late Cenozoic mammalian faunas in this region with emphasis on the hominoid evolution in Southeast Asia. During the field seasons of January 2000 and December 2001, we discovered two hominoid specimens (an upper molar and a fragment of a lower molar, respectively) from a lignite mine at Chiang Muan, northern Thailand. The upper molar is a right M1 or 2, heavily worn, with the paracone missing. The lower molar preserves only the mesial cusps (protoconid and metaconid) but it is unworn. The age of Chiang Muan

is estimated as the latest Middle Miocene (11-12 Ma), based on the associated mammalian fauna. The two specimens may be separated temporally by several hundred thousand years as they were collected from two different units of lignite (Upper and Lower Lignites). However, both molars are within intraspecific size variation, similar in dental size to modern orangutans. The general morphology of these two specimens looks similar. The cusps are low and voluminous with relatively thick enamel and low relief of dentine/enamel junction. The cingulum is very weak or absent. Because of the poor preservation of the present specimens, it is premature to assign them to some particular taxon (or taxa), and we think it better to tentatively call them as "Chiang Muan Hominoids". These are, however, the first discovery of large-bodied Miocene hominoid fossils from Thailand (and Southeast Asia as well), which indicate that large-bodied hominoids already dispersed into the Indochina peninsula by the latest Middle Miocene. Although the present specimens are fragmentary, they are the first step towards understanding the hominoid evolution in the Neogene Southeast Asia.

Ape lower molars with chimpansee- and gorilla-like features from the late Middle Miocene and late Miocene of Kenya: Implications for the chronology of the ape-human divergence and biogeography of Miocene hominoids

Martin Pickford[1] and Brigitte Senut[2]

[1]Chaire de Paléoanthropologie et de Préhistoire du Collège de France, GDR 983 et UMR 8569 du CNRS, 8, rue Buffon, 75005 Paris

[2]Laboratoire de Paléontologie du Muséum National d'Histoire Naturelle, GDR 983 et UMR 8569 du CNRS, 8, rue Buffon, 75005 Paris

This paper deals with two ape-like teeth from the Late Middle Miocene (12.5 Ma) and Late Miocene (5.9 Ma) of Kenya. An unworn, isolated lower molar from Member B of the Ngorora Formation (12.5 Ma), Tugen Hills, Kenya, differs markedly from lower molars of Middle and Early Miocene large hominoids, suggesting that it is derived away from the generalised Miocene hominoid grundplan (voluminous cusps, restricted occlusal basins, buccal cingula more or less well developed, cusps not peripheralised). Chimpanzee molars show similar derived morphology, (peripheralised cusps, bucco-lingually compressed lingual cusps, thin enamel, large and deep occlusal basin, reduced buccal cingulum) suggesting that the Ngorora specimen may belong to the same clade as chimpanzees. If so, then the implications of the tooth are important for estimating the timing of the dichotomy between chimpanzees and hominids which would be several million years earlier than is currently estimated by most researchers.

An incomplete, unworn isolated lower molar from the Kapsomin Member of the Lukeino Formation (5.9 Ma), Tugen Hills, Kenya, is most similar, but not identical, to lower molars of *Gorilla gorilla*. It is a large tooth (md 14 mm) with peripherised cusps, bucco-lingually wide distal fovea, fairly voluminous trigonid basin and wrinkled, slightly thin enamel (1.6 mm on the hypoconulid) and high dentine penetrance, all features which suggest affinities with gorillas. The main difference between this tooth and those of gorillas is the narrow slit-like lingual notch. It differs markedly from lower molars of *Orrorin tugenensis*

which occurs at the same site, which are smaller, have thicker enamel (1.8-1.9 mm on protoconid and metaconid), more centralised buccal cusps, smaller trigon basin, a minute distal fovea and low dentine penetrance. It differs from teeth of australopithecines for much the same reasons, even if its dimensions overlap with those of *Australopithecus antiquus* and *Praeanthropus africanus*. It is very divergent from chimpanzee teeth, not only in its dimensions, but also in its morphology. If the species from which this tooth came is part of the gorilla clade, then it has important implications for the timing of events in gorilline evolution, and makes it unlikely that European genera such as *Ouranopithecus* are ancestral to African apes.

The two ape teeth from Ngorora and Lukeino suggest strongly that the extant African apes evolved in Africa, and did not immigrate into the continent from Europe or Asia. *Orrorin* suggests the same for hominids in the strict sense of the term (hominoids with anatomical changes related to habitual and obligate bipedalism related to that of extant humans), meaning that the lineages leading to both the extant African ape genera as well as the hominids originated in Africa rather than Eurasia.

The Orangutan fossils in Vietnam

Vu The Long

Anthropological and Palaeoenvironmental Departerment, Institute of Archaeology of Vietnam

Among the apes, orangutang is one of the important kind of apes in Asia still exit their fossils in many Pleistocene layer . Vietnam is one of countries in South East Asia have a good collection of orangutang fossils from Pleistocene to Holocene.

The paper present:

- The distribution of orangutang fossils in Vietnam and their chronology.
- The variation of orangutang fossils in the Pleistocene collection
- Some hypotheses about the migration of orangutang from the Mainland continental Asia to the islands of South East Asia.

Hominidae other than Ponginae in eastern Asia: an updated survey

Eric Delson

Lehman College and the Graduate School, City University of New York and American Museum of Natural History

In 1992, I reviewed the presence of "dryopithecines" in Asia for an American Museum of Natural History workshop on Miocene apes. In the decade since then, we have learned more about many of the putative pongines from eastern Asia, but little about the smaller, apparently thin-enameled forms which I tentatively placed in Dryopithecinae. On the other hand, studies by Beynon, G Schwartz and Shellis have demonstrated that enamel thickness *per se* is not taxonomically diagnostic, having altered in parallel during hominoid evolution. Other authors have used a variety of characters to allocate taxa or samples to the Ponginae (*Pongo* and close relatives) or other putative clades.

About half a dozen specimens from China, India and Pakistan have been considered to represent a clade other than Ponginae. Pilgrim (1927) described a worn and mesially damaged isolated lower molariform tooth from Hari Talyangar (India) as *Hylopithecus hysudricus*; fossils from this area are now thought to date mainly between 9-7 Ma. The specimen was said to be a dP_4, but may well be an M_2. Two damaged partial mandibles from late Chinji horizons (ca. 11.5 Ma) in Pakistan were at first referred to "*Ramapithecus*" and later transferred to the new species *Sivapithecus simonsi* Kay, 1982. An additional corpus fragment with P_4-M_1 and an isolated $M^{1?}$ from near Khaur, Pakistan (ca. 8 Ma?) were briefly described by Von Koenigswald (1983). Most recently, Xue & Delson (1988[1]) described the species ?*Dryopithecus wuduensis*, based on a partial corpus with mainly damaged teeth from Longjiagou (Wudu county, Gansu province), China. It appears most similar to species usually assigned to *Dryopithecus* from European localities, but at 8-6 Ma, "Wudu" is younger than its possible western congeners.

Xue & Delson (1989) argued that the apparently thin enamel of *S. simonsi* militated against its inclusion in *Sivapithecus*, and they suggested that all the above specimens could be

broadly considered as "dryopithecines". The most recent revision of *Sivapithecus*, by Kelley (2002) does not include *S. simonsi* among the species of that genus nor in fact mention any of these Siwalik specimens (they are also passed over by Begun, 2002, in his review of European and West Asian taxa). With the removal of enamel thickness as an indicator of taxonomic affinity or plesiomorphy, there are no clear features which link the various samples to each other or to European *Dryopithecus*. Differences in premolar shape have not been sufficiently well studied to distinguish among potential clades. Nonetheless, these specimens appear to be best grouped apart from the thick-enameled pongines pending further analysis.

Another East Asian taxon often placed with the Ponginae is *Lufengpithecus*, now generally recognized from three main Yunnan Miocene populations (or species): Xiaolongtan (Keiyuan county), Shihueba (Lufeng county) and Zhupeng/Xiaohe/Leilao (Yuanmou county). Both Begun (2002) and Kelley (2002) include this genus with *Sivapithecus* and *Ankarapithecus* (and possibly *Gigantopithecus*) as orangutan relatives. Kelley did not give clear reasons for this placement, but Begun offered several cladograms based on computerized analysis of character states not detailed in this article. Harrison et al. (2002) also suggested that *Lufengpithecus* could be a pongine but also accepted the alternative that it was a primitive hominoid, perhaps belonging to Dryopithecinae (which we interpret similarly).

I agree with Begun's argument that computer-parsimony cladograms are best employed as guides to phylogeny reconstruction rather than as strict determinants of most parsimonious outcomes. On that basis, I question the likelihood of a clade *Lufengpithecus* (*Ankarapithecus* (*Sivapithecus*, *Pongo*)). The broad interorbital pillar of *Lufengpithecus* and its apparent lack of a maxillary sinus extending up into the frontal are plesiomorphies compared to the derived states in *Pongo*, *Sivapithecus* and (at least for the former) *Ankarapithecus*. Harrison et al. (2002) list a number of other plesiomorphic conditions in *Lufengpithecus*. They and other researchers cite the presence of highly crenulated enamel in *Lufengpithecus* as potential link to *Pongo*, and they also mention the small size of I^1 compared to I^2, a feature which Kelley (2002) notes has no phylogenetic weight following recent studies of its variability. If *Lufengpithecus* were to be linked to *Pongo* on the basis of its highly wrinkled molar occlusal surfaces (which appear different in detail from those of orangutans),

the transformation series pattern for this feature as well as for subnasal morphology, interorbital distance and other characters would have undergone complex homoplastic reversals.

I prefer to interpret *Lufengpithecus* as an eastern representative of the conservative hominid "stock" which existed before the split between Ponginae and Homininae (the African ape-human clade). I continue to recognize European *Graecopithecus* (including *Ouranopithecus*) as the earliest yet known member of the latter clade. Eurasian *Dryopithecus* and *Oreopithecus* appear to represent other conservative hominids, within a subfamily Dryopithecinae. The east Asian small hominids such as *?D. wuduensis*, as well as *Lufengpithecus*, could also be included in that probably paraphyletic taxon. If, in fact, *Oreopithecus* is placed there correctly, the senior name for the subfamily would be Oreopithecinae Schwalbe, 1915. Alternatively, if Begun (e.g., 2002) is correct in viewing European *Dryopithecus* as a hominine, the Oreopithecinae would only include *Lufengpithecus* and the small Asian hominids noted above, in addition to its type genus.

[1] The species was originally described in the Chinese version of this paper, published in 1988, but the English version of 1989 is more likely to be accessible to most readers.

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Evolutionary history of colobine monkeys in the Transbaikalian Province

Evgeny Maschenko

Paleontological Institute, Moscow, Russia.

The colobine monkey from the Southern Transbaikalia (Buriat Republic, the Udunga locality) is the northernmost primate ever recorded in Eurasia. Besides, it is a single find of the primate known in Siberia. Abundant materials from the Udunga locality provided a basis for distinguishing a new colobine genus, *Parapresbitys eohanuman* Kalmykov et Maschenko. Previously, in 1975, the two lower jaws and two fragments of limb bones of the colobine were found in the Shamar locality, Northern Mongolia; these were later described as *Presbitys eohanuman* Borissoglebskaya, 1981. Re-examination of the Shamar material allowed to show that the Transbaikalian colobine bears similarity with recent *Rhinopithecus* rather than with *Presbitys* and does not represent the subgenus of *Dolichopithecus*. The Udunga's forest mammalian assemblage corresponds to the Pliocene climatic optimum and is dated by the Middle Pliocene (MN 16, 3.2-2.9 m. y.). The Shamar assemblage, formed by the typical open area inhabitants, is assigned on paleomagnetic data to the boundary of the Gauss-Matuyama episodes (approximately 2.6-2.4 m. y.; Late Pliocene). The distinguishing of *Parapresbitys* gen. nov. is justified by its rather clear morphological differences from other Asiatic colobines. The genus is the largest representative of the Colobinae in Asia as seen from the following measurements: length of $M^3 - P^3$, 44.5 mm (male); $M_3 - P_3$, 52 mm; the height of alveolar process of the maxilla (pr-ns), 12 mm. The upper incisors with their mesiodistal diameter being less than buccolingual; they incisors form the angle of 40-45° with the anterior surface of the alveolar process of the maxilla. The spade-shaped pattern of the upper and lower incisors is very strongly expressed. Lateral folds of the enamel and the enamel protrusion at the base of lingual surface of the incisors form the enamel pockets. On the labial side of the incisors the enamel is 1.2 mm; on the mesial side it forms vertical folds. $P^3 - P^4$ are displaced buccally with respect to M^1 - M^3. Between $P^3 - P^4$ row and line M^1 - M^3 on the buccal surface of alveolar process of the maxilla a curvature is developed. The canines are oval in cross

section and medium-sized (in the male). M^3 shows no reduction of distal part of its crown. The new genus differs from *Dolichopithecus* in the deep relief of the molars, in the weak slope of the buccal pair of the molar cusps to each other, in larger incisors with strongly accentuated relief, along with the incisor division of the maxilla and the lower part of the cranium being very short and broad, the supraorbital torus elevated, and the bregma positioned extremely close to the sutura sagittalis.

By the morphology of the incisors, canines and premolars, the structure and shape of the corpus mandibulae, unreduced M^3 and M_3 and large body size *Parapresbitys* is similar with recent *Rhinopithecus roxellana* and Early Pleistocene *Rhinopithecus lantianensis*. The oldest finds of *R. roxellana* from Central China are dated by the latest Early to Middle Pleistocene, but possibly are even younger in age. *R. lantianensis* from Shaanxi Province (the Gongwangling locality) is dated by the Early Pleistocene. *R lantianensis* belongs to the stegodont mammalian fauna typical for the Early Pleistocene of China. This colobine monkey has the body size similar with that in *Parapresbitys,* in particular: length of $M_3 - P_3$, 50 mm (male); $M^3 - P^3$, 34.6 mm. However, the colobine from Transbaikalian is 2 m.y. elder than *R lantianensis*. The latter differs from *Parapresbitys* in the more markedly expressed bunodont pattern of the molars. In this respect, *Parapresbitys* is even closer to *R. roxellana*. The colobine from Japan (the Nakatsu locality, Yokohama province) is similar in age with *R. lantianensis*. It is dated within the range 2.7-2.5 m.y. and equally accompanied by the finds of large mammals of the stegodont community. In all, the Japan monkey, *R. lantianensis* and *Parapresbitys* show only minor differences in the structure of the incisor-bearing division of the maxilla, the molar morhology, the shape and position of the infraorbital torus and the body size ($M^3 - P^3$ is about 37 mm). Until now, the evolution and radiation of the Colobinae in Asia during the Pliocene remains as much difficult problem to solve as the origin of the very family Cercopithecidae. The oldest (Late Miocene) Colobinae in Asia is known from Afghanistan (the Molayan locality). Judging by the only find of the *Mesopithecus* lower jaw, it may be supposed that Central Asia could have been a province of the Mediterranean population area of the Colobinae. This find demonstrates the limits of the maximum dispersal of *Mesopithecus* in Central Asia. The younger colobine finds in South Asia dated by the Late

Miocene – Early Pliocene transition (about 5 m.y.) are those from China (the Mahui Formation, Yushe Basin), Northern Iran (the Maragha locality) and Pakistan (Siwaliks). These fossils, comprising just a few teeth, may belong to *Mesopithecus* (?).

The next following stage in the Colobinae evolution is documented in Southern Siberia and Japan, fromwhere only the «rhinopithecomorph» group is known. The gap between the Late Miocene and the time of appearance of the younger colobines in Asia is about 1.5-2 m.y. The record of other colobine groups in Asia relates to the later time, i.e. the latest Middle Pleistocene – beginning of Late Pleistocene. These data seem to suggest that the «rhinopithecomorphs» were the earliest colobines in Asia. Their morphology demonstrates that phylogenetically they stand far apart from the *Mesopithecus* lineage. There are reasons to believe that the appearance of the earliest «rhinopithecomorphs» in Asia much preceded the Early - Middle Pliocene transition. The «rhinopithecomorph» branching off from the common stem of the Colobinae has taken place even earlier. An extensive spatial and temporal distribution of the group, along with the polymorhism of its members suggest the long-term evolution of the «rhinopithecomorphs» in Asia. . There are two ways to reconstruct this evolution. The group might have originated in Africa and soon have gone extinct on that continent, which was preceded by its spreading to Asia. Or, alternatively (which seems more likely), it represents a specific colobine branch, which experienced a very fast evolution somewhere at the margin of the Colobine population area (in Asia?) already after the invasion of its ancestors from Africa. Paleontological data suggest that some part of the evolution of this group took place in Asia and that phylogenetically it is separated from another colobine linage (*Mesopithecus* and *Dolichopithecus)* whose evolution proceeded in the Mediterranean. During the Pliocene the dispersal areas of the Colobine of the Mediterranean - East Asiatic provinces already showed no overlap, so that the evolution of both lineages run in parallel. The separation of the «rhinopithecomorph» branch resulted from its early specialisation within the Colobinae. By the morphology of the face skeleton, the symphyseal portion of the mandible and the tooth pattern, *Parapresbitys eohanuman*, *Rhinopithecus lantianensis*, and *R. roxellana* are closer to African *Colobus* and *Rhinocolobus,* rather than to the *Mesopithecus* - *Dolichopithecus* lineage. The presence of common peculiarities in the morphology of the

early Pliocene Colobinae from Africa and the «rhinopithecomorphs» from the Middle to Late Pliocene of Asia, along with the datings of Asiatic finds, warrant to substantiate the above-suggested scenario of their evolution.

Forest Refugia and the Evolution of Primates During the Tertiary and Quaternary in East Asia

Nina G. Jablonski

Department of Anthropology, California Academy of Sciences, Golden Gate Park, San Francisco

The primates of Asia derive from three major Tertiary radiations, which occurred in the Early to Middle Eocene (adapids, omomyids, tarsiers, early anthropoids), the Early to Middle Miocene (hominoids), and the latest Miocene to Early Pleistocene (cercopithecoids), respectively. To our knowledge, these radiations were largely confined to rainforest and evergreen broad-leaved forest environments. Some of these biomes, such the rainforests of Southeast Asia and the Hengduan Mountains and Sichuan Basin of China, were protected to a great extent from environmental deterioration (at the Eocene-Oligocene boundary, in the latest Miocene, and in the latter Pleistocene) by their latitude or by the conformation of landforms relative to prevailing monsoon winds. This created a situation in which certain adapid, tarsier, ape, and monkey species could survive in selected refuges while becoming extinct elsewhere. These refuges became "museums" of paleoendemic taxa and areas of high overall biodiversity. Species of tarsiers, gibbons and monkeys, which originated respectively in three the major Tertiary radiations, can still be found together in the rainforests of Borneo, Sumatra and Java. In this paper, the importance of forest refuges in the evolution of primates in Asia will be discussed with emphasis on the lineages of the tarsier, gibbon, and snub-nosed monkey.

A Pliocene Colobine Skull from the Nakatsu Group, Kanagawa, Japan

Mitsuo Iwamoto[1], Yoshikazu Hasegawa[2], and Akihiro Koizumi[3]

[1]Japan Monkey Centre, Inuyama, Aichi, Japan

[2]Gunma Museum of Natural History, Tomioka, Gunma, Japan

[3]Iida-City Art Museum, Iida, Nagano, Japan

In December, 1991, one of us, A. Koizumi who was a young paleontologist of Yokohama National University, collected two lumps of rock containing some teeth of any fossil mammal at a former gravel quarry site known for the place name of Kosawa in Kanagawa Prefecture, Central Japan. Next month, he noticed that it seemed to contain a fossil skull of a monkey. After the cleaning of it, we could consider it to be apparently the skull of a colobine monkey.

The site is situated at the right bank of the Sagami River which runs through the Sagami plains, and geologically it belongs to the Kanzawa Formation, the Nakatsu Group in Kanagawa Prefecture, Japan. The Nakatsu Group is a Late Pliocene sequence as a whole, and the Kanzawa Formation is the lowest level among it (about 250 myBP).

The discovered skull is a calvaria of a adult male monkey without the lower jaw. The most of its facial part and palate are well preserved with right C and P4-M3 and left M2 and M3, but the cerebral part is lacking except frontal portion. The canine is big and the molars have a typical colobine type morphology: i.e. increased crown relief. The face of the specimen is long, comparing with relatively short face of colobine monkeys in genaral.

Already in 1994, Delson commented on this specimen as follows.

"This fossil could belong to the same species based on tooth size and morphology, and the face is not dissimilar to that expected for a male *Dolichopithecus* (*D. ruscinensis* by Depéret, 1889)."

Surely it resembles well the male specimen by Depéret and therefore could be recognized to belong to the genus *Dolichopithecus*. On the other hand, however, it is fairly different from the specimen by Depéret in some morphological features. One of unique

features of the skull from the Kosawa locality, for example, is very thin lateral rims of orbits (the frontal edges of postorbital plates). Thus the newly discovered skull seems to be recognized as a new species of *Dolichopithecus*

ABSTRACTS (Poster Session)

The Late Cenozoic Irrawaddy Formation (Myanmar) and its mammalian fauna

Chit Sein[1] and Thaung Htike[2]

[1]Department of Geology, University of Yangon, Myanmar

[2]Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

We briefly review the stratigraphy and mammalian fauna of the Late Cenozoic Irrawaddy Formation, Myanmar. The Irrawaddy Formation, which is more than 3000 m in total thickness, consists of fresh-water sediments formed as low energy fluvial channel to strong energy over bunk deposit. It contains many terrestrial vertebrate fossils including total 28 mammalian genera of three orders (four genera of Proboscidea, five of Perissodactyla, and 19 of Artiodactyla). The Irrawaddy Formation is subdivided into lower and upper parts, and the two can be distinguished from one another based on the lithology. The lower part, which is about 1600 m in thickness, is characterized by more arenaceous, false bedded, massive, ferruginous sandstones intercalated by several consolidated red residual soil layers and by silty clay. Vertebrate fossils are relatively rare. Its mammalian fauna consists of seven genera (one rhinocerotid, one equid, one suid, two Giraffid, and two bovid genera) and is correlated to that of the late Miocene to Pliocene Dhok Pathan Formation of the Siwalik Group in Indo-Pakistan. The upper part, which is more than 1400 m in thickness, is characterized by loose, friable, poor to moderately sorted, coarse-grained sandstones and conglomerates, with large cross stratification and large amount of sandstone nodules. It yields abundant vertebrate fossils. Its mammalian fauna consists of 21 genera (three stegodontid, one elephantid, one rhinocerotid, two equid, one anthracotheriid, two hippopotamid, one suid, one cervid, and nine bovid genera) and is correlated to that of the early Pleistocene Pinjour and Tatrot Formations of the Siwalik Group.

Biogeography of hyaenodontid creodonts in Paleogene Asia

Naoko Egi[1], Takehisa Tsubamoto[1], Patricia A. Holroyd[2], Nobuo Shigehara[1], Masanaru Takai[1]

[1]Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan

[2]Museum of Paleontology, University of California, Berkeley, CA 94720, U.S.A.

The Hyaenodontidae (Creodonta) is a group of archaic carnivorous mammals existed from late Paleocene to middle Miocene. Its fossil records are known from North America, Europe, Africa, and Asia. Our knowledge on Asian hyaenodontids was based on Chinese and Mongolian materials and on a few Indo-Pakistan genera until some materials were found from Myanmar and Kyrgystan recently. This study summarizes the present occurrences of fossil materials and discusses paleobiogeography of Asian hyaenodontids.

Hyaenodontids are taxonomically diverse group, and can be separable into four to seven subfamilies. The proviverrine and limnocyonine materials from central and northern China and Mongolia have been assigned into the genera known from early to middle Eocene North America. Other materials from this area have been considered to belong to the subfamily Hyaenodontinae, although generic classification has not been settled for some materials. The recent discoveries of primitive hyaenodontines from central Asia extends the distribution of Asian hyaenodontines to further west. Proviverrines are also known from South and Southeast Asia; however, unlike the Chinese forms, they are endemic to the area and are considered to be closely related to the one known from North Africa and southern Europe. The recent findings in Pakistan and Myanmar provide an evidence that these advanced proviverrines were common and diversified in the area since Eocene. The distribution of pterodontines overlaps with that of advanced proviverrines, but they are more widely spread in whole southern part of Asia, known also from southern and central China.

The current data suggests that the Asian hyaenodontids can be divided into northern and southern assemblages. Among the northern assemblage, limnocyonines and proviverrines suggest immigration events from or to North America, and hyaenodontines indicate a

connection with European forms. The southern assemblage consists of advanced proviverrines and pterodontines, and their distribution indicates dispersal of hyaenodontid creodonts around Tethys Sea.

Review of the fossil primates of Eastern Eurasia (Russia and adjacent territories)

Evgeny Maschenko

Paleontological Institute, Russian Academy of Sciences

The early history of the order Primates from the Eastern part of Eurasia reflects restructurisation of mammalian faunas of Eurasia and North America than occurred on the Paleocene-Eocene border about 57 m.y. ago. The appearance of Primates in Asia is connected with the advent of certain groups of American mammals to Asia. The most ancient finds of Primates from Asia are dated Early Eocene (the Tsagan Khushu locality, Mongolia, Southern Gobi). This is the most ancient and the only Asian representative of family Omomyidae. *Altanius orlovi*, one of the smallest and specialized representatives of Primates. It is discriminated by a reduced talonid of P_4. Metaconid is well expressed. The M_1 trigonid is open, paraconid cone-shaped and not reduced. The M_3 has a large paraconid displaced lingually and elongated talonid. Additional studies of *A. orlovi* reveiled two forms (species?) with similar dental morphology that differ in size only. The status of the larger form of *Altanius* sp. may be determinate more precisely when more data are obtained on variability and sexual dimorphism of the species. Primates became a frequent component of mammal faunas from these territories the Late Miocene (Late Turolian, MN 11-13, about 8 m.y.). In terms of zoogeography, the territories of the south of Eastern Europe, Trans-Caucasus and Central Asia make part to the Mediterranean Province and the taxonomic composition of primates during this time span does not differ much from typical Mediterranean, but for some species (endemic). During Late Miocene not very numerous apes became extinct here: Dryopithecidae, one genus, one species, and Pliopithecidae (?), one genus, one species, and Cercopithecidae becomes common: subfamily Colobinae, one genus, two species. In 1908 Prof. V.D. Laskarev reported a finds of *Oreopithecus* sp. from Kalfa locality (Moldavia, Late Turolian). The material on which the communication was based, was later lost. However, given that the Oreopithecini tribe is endemic to Central Italy, these date may by unreliable. So, by the beginning of the Ruscinian, no hominoid representatives are known from the territory

considered, whereas the Cercopithecidae became numerous.

In the end the Cercopithecidae became a common component of the zonalasseblages of hypparion faunas in Moldavia, Ukraine, Georgia, Northern Iran and Afganistane. Colobinae: Ukraine, the Grebeniki 1 locality - *Mesopithecus ucrainicus*; Afghanistan, the Molayan locality -*M. pentelici*; Northern Iran, the Maragha locality - *Mesopithecus* sp. Dryopithecidae are known from Georgia, Udabno locality – *Dryopithecus garedzianus*. An isolated deciduous P^4 previously assigned to *Pliopithecus* sp. was discovered in Morskaia 2 locality (Rostov Province, Russia, Northern sore of Azov Sea) in 2002 (table 1). Out of the 6 known localities, the Hominoidea (2 localities) and Colobinae (4 localities) are present. The taxonomy of primates from Kalfa locality is remain uncertain. From Pliocene (Ruscinian) and Pleistocene of Russia (Transbaykalian Province), North Mongolia, Ukraine, Moldavia and Tadjikistan representatives of Cercopithecidae are known, including two subfamilies Cercopithecinae - 2 genuses, 4 (?) species and Colobinae - 2 genuses, 3 species. From the territories of Russia and boundary countries 11 localities of this age with remains of Cercopithecidae monkeys are known altogether. Chronological distribution of Cercopithecidae from these localities is beginning the end of early Pliocene (MN 14, 4.5 m.y.) up to middle Pleistocene (0.35 m.y.) (Table 1). In Moldavia and Ukraine Cercopithecidae make part to Moldavian (Ruscinian) and Chaprovian (Early Villafranchian) mammals assemblages. One genus of Cercopithecidae present in the Late Pliocene of Tadjikistan was the Asiatic analogy of the Late Chaprovian (Middle Villafranchian) mammal assemblages. Cercopithecidae from Western Transbaykaliaan (Russia) were part of the Early-Middle Villafranchian mammal assemblages. The only and single representative of Cercopithecina is known from the Middle Pleistocene of Georgia - genus *Macaca*, a Caucasian analogy to the Cromerian (Warm stage of Mindel or Interglacial IV).

In the Late Ruscinian of Southern Moldavia and Ukraine both subfamilies of Cercopithecidae co-exist: Colobinae (1 genus and 2 species: *Dolichopithecus ruscinensis*, *D. hypsulophus*) and Cercopithecinae (1 genus: *Macaca* perhaps including 2 species). Cercopithecinae and Colobinae are known together from at least two localities dated as Latest Ruscinian of Ukraine – Novopetrovka locality, Moldova - Budey locality (Table 1).

Beginning the second half of the Late Pliocene (from MN 16) the only Cercopithecinae subfamily is present in the South of East Europe and in Tadjikistan. Stratigraphical distribution of the genus *Dolichopithecus* in the South of Ukraine is most probably limited to ages 2.2-2.4 M y. From Late Ruscinian (?) - Early Villafranchian of Ukraine a species smaller than *D. ruscinensis* species, *D. hypsulophus*, is known. From *D. ruscinensis* it differs insignificantly in the structure of C-P_4 complex, in morphology of symphiseal part of lower jaw and relatively smaller lower incisors. In the Late Pliocene-Early Pleistocene of Ukraine and Moldavia genus *Paradolichipithecus* is not known. In the Late Pliocene of Middle Asia (Tadjikistan, Kuruk-Say) a representative of genus *Papio* is reliably determined. *Papio (Paradolichopithecus) sushkini* is a specialised representative of this genus. It is a medium-sized and differs from other extinct and modern *Papio* in large bunodont molar teeth and in thick enamel. At Transbaykalian and Mongolia on the border of Early-Middle Pliocene only Colobinae (*Parapresbitys eohanuman*) is present and Cercopithecinae is absent. The latter Cercopithecinae appear in China and Korea in the Middle Pleistocene. *P. eohanuman* is a representative of the group of "Rhinopithecomorphs" colobines, widely spread in Asia (Transbaykalian, Mongolia, Japan, China) in the end of the Middle Pliocene-Early Pleistocene. It is the largest representative of Colobinae, characterised by robust upper and lower incisors. Enamel on the labial surface of incisors has well developed shovelling. The lingual surface of incisors has an enamel pocket formed by lateral enamel folds. M3 has non-reduced distal pair of main cusps. The dentition of *P. lantianensis* is relatively close to that in modern *Rhinopithecus roxellana* and *R. eohanuman* is from Early Pleistocene of China. Middle Pleistocene representative of cercopithecine subfamily from Georgia (*Macaca* cf. *sinica*), in the morphology of molars is closer to the Asiatic *Macaca* of the species group "*sinica*", than European representatives of the genus *Macaca*.

Table 1. Chronological distribution of Primates in Miocene-Pleistocene of Russia and adjacent countries

Ages		M.y.	Country and localities	Mammal ages		Systematic groups of the Primates	
						Cercopithecinae (or Hominoidea)	Colobinae
Pleisto-cene	Late	0.35	Georgia (Kudaro 1)	----------	Mindel	*Macaca* cf. *sinica*	-
	Middle						
	Early	1.85					
Pliocene	Late	2.2	Tadjikistan, Kuruk-Say	Villafranchian	MN 16	*Papio suschkini*	-
		2.2 - 2.4(?)	Ukraine, Kotlovina		MN 16(?)	-	*Parapresbytis eohanuman*
		2.6 - 2.4	Mongolia, Shamar		MN 16(?)	-	*Dolichopithecus* cf. *ruscinensis*
	Middle	3.2-2.9 (?)	Transbaykalian, Udunga		MN 16(?)	-	*Parapresbytis eohanuman*
		2.6 - 3.4	Moldova, Gavanosa		MN 15	*Macaca* sp.	-
			Moldova, Cebrikovo		MN 15	*Macaca* sp.	-
	Early		Ukraine, Voynichevo		MN 15	-	*Dolichopithecus hypsulophus*
		3.5 (?)	Moldavia, Budey	Ruscinian	MN 14/15	*Macaca* sp.	*Dolichopithecus ruscinensis*
			Ukraine, Grebeniki 2		MN 14/15	*Macaca* sp.	-
		4.5	Ukraine, Novopetrovka Iran, Maragha		MN 14	*Macaca* sp.	*Dolichopithecus ruscinensis* *Mesopithecus pentelici*
Miocene	Late	5.3	Russia, Morskaia 2 Ukraine, Grebeniki 1 Afghanistan, Molayan	Turolian	MN 13	*Pliopithecus* sp.	*Mesopithecus ucrainicus* *Mesopithecus* sp.
			Georgia, Udabno		MN 12	*Dryopithecus garedzianus*	
			Moldavia, Kalfa			Primates gen ind.	
		8.3			MN 11		

Neogene mammalian biostratigraphy and age of fossil ape from Thailand

Hideo Nakaya [1], Haruo Saegusa [2], Benjavun Ratanasthien [3], Yutaka Kunimatsu [4], Shinji Nagaoka [5], Pratueng Chintaskul [6], Yusuke Suganuma [7] & Akira Fukuchi [8]

[1]Department of Earth and Environmental Sciences, Kagawa University, Takamatsu, 761-0396, Japan

[2]Institute of Natural and Environmental Sciences, Himeji Institute of Technology, Sanda, 669-1546, Japan

[3]Department of Geological Sciences, Chiang Mai University, Chiang Mai, 50200, Thailand

[4]Research Institute of Primatology, Kyoto University, Inuyama, 484-8506, Japan

[5]Department of Geography, Nagasaki University, Nagasaki, 852-8521, Japan

[6]Department of Geography, Rajabhat Institute, Nakhon Ratchasima, 30000, Thailand

[7]Ocean Research Institute, University of Tokyo, Tokyo, 164-8639, Japan

[8]Department of Earth Sciences, Okayama University, Okayama, 700-8530, Japan

The joint Japan-Thailand expedition surveyed the Neogene basins in Thailand from 1996 to 2002. The Neogene sediments in Thailand yield many vertebrate including great ape fossils. Mammalian faunas from Thailand resemble those from the Early to Middle Miocene of the Siwaliks according to previous works. We examined the vertebrate fauna of the Neogene sites, Mae Soi, Li Basin, Pong Basin, Mae Moh, Chiang Muan, Had Pu Dai and Sop Mae Tham of Northern Thailand, and Nakhon Ratchasima of Northeastern Thailand.

At Mae Soi 50km south west of Chiang Mai, a primitive amebelodontid gomphothere, *Archaeobelodon*, and equids were collected. This assemblage suggests that the Mae Soi Fauna is the late Early Miocene in age.

At Chiang Muan Lignite Mine 150km east of Chiang Mai, we found fossils of ape, suinaes, and a primitive tetralophodont gomphothere, *Tetralophodon* cf. *xiaolongtanensis*. Chiang Muan great ape fossils are the first record from the Neogene of Southeast Asia. The mammalian fauna from the Chiang Muan Formation suggests the latest Middle Miocene age.

At Sop Mae Tham, we found a new Late Miocene fauna. It includes the Hipparionini (Equidae), which has never been recorded in the Neogene of Southeast Asia. The Sop Mae Tham mammal fauna consists of tetralophodont gomphotheres, rhinocerotid, hipparionin equids, *Listriodon* and suinae, tragulids, Boselaphini and primitive bovids. This mammalian assemblage suggests the early Late Miocene age.

We found new Neogene mammalian faunas from a number of sand pits in Tha Chang area near Nakhon Ratchasima. The Middle Miocene mammalian fauna consists of amebelodontid gomphothere, *Gomphotherium* and *Prodeinotherium*. The Latest Miocene to Early Pliocene fauna yields *Hipparion*, primitive *Stegodon, Stegolophodon* and primitive *Merycopotamus*. The Early Pleistocene fauna yields advanced *Stegodon*.

It has been made clear that the previous age of mammalian faunas in Thailand were mostly correlative with the Early to Middle Miocene, but the mammalian ages of some new faunas are equivalent to the Late Miocene and Pliocene-Pleistocene. We propose the Neogene mammalian biostratigraphy in the Southeast Asia. We continue to survey mammalian faunas, stratigraphy, and magnetostratigraphy in the Neogene sites of the Thailand, also. Especially, we would like to excavate sand pits and gravel dump from sand pits in Tha Chang area near Nakhon Ratchasima, and establish stratigraphy and age of each sand pits from the in situ mammalian fossils.

Structure of the two maxillae of *Pondaungia cotteri* from central Myanmar

Nobuo Shigehara, Masanaru Takai, Takehisa Tsubamoto, Takeshi Nishimura & Naoko Egi

Primate Research Institute, Kyoto University

A specimen of *Pondaungia* (NMMP-KU 0003) from the late middle Eocene Pondaung Formation in central Myanmar includes maxillary fragments and parts of the dentition, some hitherto undocumented. We also found another maxilla of *Pondaungia* (NMMP-KU 1557) in 2002 field research in Myanmar.

Pondaungia has a large spatulate 11 closely resembling that of crown anthropoids. It possesses a stout projecting upper canine (like anthropoids) but differs from that tooth of crown anthropoids in lacking a strong mesial groove. There are three upper premolars of which P2 is distinctly smaller than P3 or P4. P3 has a buccolingually oriented mesial profile and an inflated distal profile resembling that of parapithecids and crown anthropoids. *Pondaungia* has a stout zygomatic root with a strongly demarcated muscle scar for the superficial masseter situated well above the occlusal plane. The inferior orbital margin is not preserved but the inflated suborbital region allows for the inference that the orbit was small. This specimen is not sufficiently well preserved to identify if there was postorbital closure. However, a specimen of the frontal bone of *Amphipithecus* shows that its orbital septum was absent or poorly developed. If, as commonly supposed, "*Pondaungia* and *Amphipithecus* " are sister taxa, postorbital closure was probably absent in *Pondaungia*.

The maxilla of *Pondaungia* is larger than in *Amphipithecus*. The orbital surface of the maxilla contains a shallow grove and swelling. The orbital surface of the maxilla in *Amphipithecus* also contains a shallow grove, but its surface is rather flat. This different structure in orbital surface of *Pondaungia* is also observed in a newly discovered maxilla (NMMP-KU 1557). The large incisors, molars with poorly developed crests and thick enamel, together with the stoutly developed and strong dorsal component of the force vector of the superficial masseter muscle suggest that *Pondaungia* maxilla shows an adaptation for the diet

low in fiber, but that included hard food objects like nuts or seeds.

Reevaluation of the Eocene anthracotheres (Mammalia; Artiodactyla) from the Pondaung Formation, Myanmar

Takehisa Tsubamoto, Masanaru Takai, Naoko Egi and Nobuo Shigehara

Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan

We reevaluate the classifications of the anthracotheres (Mammalia; Artiodactyla) from the primate-bearing Pondaung Formation (latest middle Eocene; central Myanmar). The three anthracotheriid genera previously known from the Pondaung Formation, *Anthracothema*, *Anthracokeryx*, and *Anthracohyus*, are synonymized into *Anthracotherium*. As many as 13 species had been recognized in the Pondaung anthracotheres, but they are summarized into four species (*Anthracotherium pangan*, *Anthracotherium crassum*, *Anthracotherium birmanicum*, and *Anthracotherium tenuis*), based on the difference of the size of lower first molars (~ the difference of body size). Dental morphology in each species indicates high variation, and the four species are not separable based on their dental morphology. The dental morphology of the Pondaung *Anthracotherium* species are distinct from that of other species and are the most primitive. In addition, the Pondaung *Anthracotherium* species are the oldest in age among the genus and they are dominant in collection size among the Pondaung mammals. The genus *Anthracotherium* might have originated and rapidly radiated around the Pondaung area during the latest middle Eocene. "*Siamotherium pondaungensis*" described from the Pondaung Formation as the Anthracotheriidae is synonymized to *Pakkokuhyus lahirii* (Artiodactyla; Helohyidae).

Faunal change from the late Pliocene Colobine Monkey bearing marine strata (Kanzawa formation) to the Canid bearing strata near the Plio-Pleistocene boundary (upper part of the Kasumi formation , Kazusa Group), Western Tokyo, Japan

Akihiro Koizumi

Iida City Museum, 2-655 Outhemati, Iida, 395-0034, Japan

The land mammal fossils from the Kanzawa formation, lower part of the Nakatu Group, is called Aikawa fauna, and is follows: Colobine monkey, Colobinae, indet. (skull, Iwamoto et al., 2003); large elephant, *Stegodon miensis* (skull, radius, metacarpus); Rhinocerotidae, indet (untiform); samber deer, *Cervus* (*Rusa*) sp. (part of antler, cervical vertebra, femeur, etc.).

The age of the Colobine Monkey bearing the Kanzawa formation, lower part of the Nakatu Group, is estimated as 2.6-2.7 Ma, according to marine micro fossils and paleomagnetism (Saito, 1988).

The land mammal fossils from upper part of the Kasumi formation, is called Akishima fauna, and is follows: a large-sized hypercarnivorous canid, *Canis* (*Xenocyon*) *falconeri* (skull and part of skeleton, Koizumi, 2003, in press); small elephant, *Stegodon aurorae* (skull, molar); deer, *Cervus* (*Nipponicervus*) *kazusensis* (antler, lower jaw); deer, *Cervus* (*Rusa*) sp. (part of antler).

The Kasumi formation is overlaid with the Hirayama formation. The land mammal fossils from the Hirayama formation is also included Akishima fauna, and is follows: small elephant, *Stegodon aurorae* (part of skeleton,Taru,1996); deer, *Cervus* sp., cf. (*Nipponicervus*) *kazusensis* (part of skeleton, Takakuwa,1997); deer, *Elaphrus* (*Elaphroides*) *shikamai* and *E.* (*E.*) *tamaensis* (part of antler, Shikama, 1964 , Otsuka&Hasegawa,1976), *Elaphrus* sp. (part of skeleton).

The Hirayama formation is overlaid with the Oyamada formation. The age of

the 2nd Horinouchi ash bed in the Oyamada formation is estimated as 1.6Ma, and so the age of the hypercarnivorous canid bearing upper part of the Kasumi Formation is estimated as 1.8 Ma front and back (Koizumi, 2003, in press).

Stegodon aurorae, inhabited from the late Pliocene to late early Pleistocene (about 2.4 – 1.2 Ma from Western Tokyo), is a small specialized endemic form, and is considered to have evolved from *Stegodon miensis* (Saegusa, 1996). So that the geographical severance of the Japanese islands from the continent probably generated this speciation (Dobson and Kawamura, 1998).

It is new result that occurrence of a large-sized hypercarnivorous canid, *Canis* (*Xenocyon*) *falconeri* at the same age inhabited *Stegodon aurorae*. So I consider that *Canis* (*Xenocyon*) *falconeri* and associated middle sized deer were immigrated from the Chinese continent, however, no evidence that proboscideans immigrated at same time.